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Fossils, Phylogeny, and Anatomical Regions: Insights Exemplified Through Turtles

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Fossils, Phylogeny, and Anatomical Regions: Insights Exemplified Through Turtles

by

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Dedication

This work is dedicated to my family. To my parents Nora and Wayne Burroughs for teaching me that the only way to achieve dreams is through hard work, but through hard work dreams can be achieved. To my sister, Angela Macias-Armstrong, who many years ago encouraged me to come to Austin to attend UT-Austin, and encouraged me to take a course taught by Chris Bell. This dramatically changed my life by helping my realize what I wanted to do and what I could do. Finally, to my wife, Catherine Burroughs, who has tirelessly supported my endeavors and without who this work would never have been completed.

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I must acknowledge the efforts of the committee who supervised this research, who committed many hours of effort on their part to improve my education, writing, and thinking about matters associated with biology and paleontology. Julia Clarke challenged me to think deeply about how methods we use as scientists affect our thinking, perceptions, and communication. She was always there to discuss any issues I had during my thesis. Her work in evaluating and improving my writing and skills as a scientist has been invaluable. I owe a great debt to Travis LaDuc, he has carefully guided me throughout my undergraduate and graduate career. He has always been careful to listen and provide critical insights when I needed them most. Those insights helped me improve as a scientist and a person. I have no doubt that I would not be here today if it weren't for his guidance and help.

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research. Each chapter holds a separate acknowledgments section where I have recognized my gratitude to those individuals who have helped bring this work to fruition.

Preface

Arguably, this work had its conception in 2008 when I began working with Chris Bell, Travis LaDuc, and Dean Hendrickson (all from UT-Austin) on a project involving the skeletal variation of the endangered Mexican box turtle, *Terrapene coahuila*. At the time, I was still an undergraduate, wandering through an Anthropology degree, but I became increasingly interested in issues associated with variation, and as a result in the biology and evolution of organisms. The impetus for evaluating *Terrapene coahuila* was two-fold. First, it was an understudied organism that continues to need attention drawn to it for conservation purposes. Second, I was after a greater understanding of box turtle morphology and variation. The latter point was because early on I had established the ultimate goal of this thesis, at least as originally conceived, to describe and name a distinct box turtle from the Eocene/Oligocene boundary of west Texas. That turtle is now described in Chapter 1 of this thesis.

After I finished my work with *Terrapene coahuila*, I took up the work now housed in Chapter 1, but with a slightly different focus. My exposure to the ideas associated with how morphological variation can impact phylogenetic analyses plagued me from the beginning of my master's work. I focused on evaluating not just the fossil, but understanding its phylogenetic affinities. As I worked harder on this problem, it became obvious that I would need to account for variation in the form of polymorphisms. Thus, the phylogenetic analyses that form up a portion of Chapter 1 were borne out through my desires to build a robust phylogeny that accounted for variation. The body of

Chapter 1 now represents not only a fossil description, but a broad phylogenetic analysis of testudinoid turtles, and brings to light real problems associated with working within this group.

At the same time as I worked on Chapter 1, I had the great fortune to take a course taught by Julia Clarke. This course revolved around the application of phylogenetic methods to paleontology. In her course, I decided I would explore an additional problem associated with reconstructing the phylogeny of organisms. That problem is a systematic bias among researchers to focus only a few selected sets of characters for inferring phylogeny. I chose to exemplify my work with both morphology and turtles. Because many turtle paleontologists struggle with having fossil specimens represented by only skulls or shells. This exemplified my own frustration from having only a shell to describe the new fossil from, in my first chapter. After the course I realized I had built a second chapter that was intimately related to the first chapter. Because both attempt to address issues plaguing phylogenetic reconstruction. This work is now the body of Chapter 2.

So, both chapters of this work were conceived somewhat independently, but are interrelated by virtue of being designed to address and attempt to solve issues associated with phylogenetic reconstruction, fossil identification, and evolutionary interpretations of testudinoid turtles. This work also reflects my evolution as a researcher from humble undergraduate beginnings to a more advanced understanding of biology, paleontology, and science in general. This work represents the conclusion of my Master of Science in Geosciences. The thesis contained hereafter was born, struggled through adolescence and

is today, I hope, a mature vehicle that serves to enlighten the reader regarding this subject matter.

Abstract

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The University of Texas at Austin, 2013

Supervisor: Christopher J. Bell

Fossils, Phylogeny, and Anatomical Regions: Insights Exemplified Through Turtles

There are more than 300 species of extant turtles, the majority of which belong to the Testudinoidea. Here I describe a new box turtle from the Eocene-Oligocene boundary of west Texas. This specimen impacts the phylogeny of Testudinoid turtles by pulling the divergence of extant Testudinoid turtles back in time approximately 25 million years. This results in a need to refocus on paleontological research of Testudinoid turtles into the late Paleogene and early Neogene to identify fossil localities and specimens that can help further elucidate the evolution of the group. New work on the fossil record of turtles also requires a re-evaluation of methods used for identifying and evaluating the evolutionary history of turtles as a group. An implicit assumption over the last 150 years of turtle paleontology was that both turtle shells and turtle heads reveal congruent and complimentary evolutionary relationships. This assumption was never adequately tested. I utilized a series of methods to evaluate the congruency of phylogenetic hypotheses using disparate anatomical regions. Using a dataset of extant Emydid turtles, I evaluated whether turtle shells and turtle heads provided congruent and complimentary phylogenetic hypotheses. My methods employed parsimony-based reconstruction, maximum-likelihood-based reconstruction, and Bayesian-based reconstruction, including Bayesian-partition analyses. My conclusions are that heads and shells do not provide fully congruent topologies, and that in many cases there is a loss of phylogenetic resolution when only turtle sklls are used to generate phylogenies. The implication is that a focus on a robust and complete dataset of anatomical features will provide the best basis for further investigation of fossils. My work also provides a framework for dataset exploration by providing a method to identify the most robust phylogenetic signal found within a dataset. This framework will allow non-turtle paleontologists and systematists the ability to further investigate their own datasets and develop robust hypotheses of evolutionary relationships across the diversity of the tree of Life.

Table of Contents

Chapter 1: Description of a new functional box turtle from the Eocene/Oligocene boundary of west Texas and issues of testudinoid phylogeny

INTRODUCTION

There are currently 328 species of extant turtles recognized today (Turtle Taxonomy Working Group 2010). Turtles currently have a worldwide distribution and terrestrial or freshwater aquatic forms are found on every continent except Antarctica. A substantially greater amount of turtle diversity is recognized as representatives found only in the fossil record. The fossil record of turtles, as compared to many vertebrates, is extensive, and fossils are found on all continents and in all time periods from the Triassic through the Holocene (Hay 1908; Młynarski 1976; De La Fuente et al. 2010).

Among extant turtles are several lineages, commonly called 'box turtles'; these do not form a natural group, but they share characteristics related to kinesis of the plastron. 'Box turtle' as a term has been used to represent two different, but related, concepts. The first concept is an anatomical or functional construct. As a functional concept, 'box turtle' refers to all turtles with a plastral hinge and anatomy consistent with the behavioral ability to pull the extremities (head, limbs, and tail) into the carapace and then, through muscle control, pull the plastral lobes closed against the carapace. Through this action the soft tissues of the turtle are sealed inside of a box formed by the bony shell. Two extant groups of turtles are box turtles in this functional sense, the Asian clade *Cuora* and the North American clade *Terrapene*. It is also in reference to these two clades that the term 'box turtle' is used as a second, taxonomic, concept. *Terrapene* are commonly referred to as 'box turtles' or 'box tortoises' (e.g., Bell 1825, Baur 1891, Hay 1908,

Milstead 1969, Minx 1996, Joyce et al. 2012), and *Cuora* are commonly called 'Asian box turtles' or simply 'box turtles' as well (e.g., Yasukawa et al. 2001, Honda et al. 2002, Ernst et al. 2008).

The dual usage of the term 'box turtle,' to represent anatomical concepts and taxonomic concepts is not particularly problematic when evaluating the extant biota. Although *Terrapene* and *Cuora* both belong to the larger clade of turtles called Testudinoidea, they are not closely related taxa, and each group has distinct characteristics and geographic distributions. This makes recognition of modern specimens of these two groups relatively easy and makes referring to them taxonomically as 'box turtles' an acceptable practice.

In addition to the extant taxa, multiple functional box turtles are known only from fossils. *Shachemys* is known from the Late Cretaceous of Asia, and is the earliest known turtle with a plastral hinge (i.e., the earliest possible functional box turtle). *Shachemys* belongs to the Adocidae, an extinct clade of turtles with a fossil record from the Cretaceous through Paleogene. The Adocidae is currently hypothesized to belong to a larger extinct clade the Adocusia. The Adocusia is hypothesized to be placed on the stem of Trionychia (Danilov and Parham 2006, Danilov and Syromyatnikova 2009, Danilov et al. 2011).

Planetochelys is a functional box turtle known from the Paleocene through the middle Eocene of North America and has been found in high abundance in the Uinta and Wastach formations (Hutchison 1980, Weems 1988, Hutchison 1992, Hutchison 1998, Holroyd et al. 2001, Hutchison 2003). At present, the phylogenetic affinities of *Planetochelys* are unknown; only the holotype, the posterior half of a carapace, is described for *Planetochelys savoei* (Weems 1988). Additional material remains undescribed, but researchers working with the taxon

hypothesize its placement within the Trionychoidea (Patricia Holroyd, personal communication 2011).

Ptychogaster is a functional box turtle known from the middle Eocene through the Oligocene of Europe and is hypothesized to belong within Testudinoidea (Claude 2006). However, *Ptychogaster* has not been included within larger phylogenetic analyses of Testudinoid turtles, and descriptions of material called *Ptychogaster*, like those of *Planetochelys*, lack in-depth analysis and description.

The issue of dual meaning does become problematic when considering the fossil record. For example, the search for the evolutionary roots of *Terrapene* (a *taxonomic* 'box turtle') in the fossil record of North America is complicated by the fact that several fossils obviously represent *functional* box turtles, yet may have nothing to do with the evolutionary lineage of *Terrapene*. In deference to the historical use of 'box turtle' as a taxonomic concept, I draw a distinction between the taxonomic and anatomical/functional concepts. I refer to the latter group as functional box turtles.

The fossil record of *Terrapene* is known to extend from the middle Miocene to the modern (for review see Dodd 2001 and Joyce et al. 2012). *Terrapene corneri* is the oldest named *Terrapene*. It was recovered from the middle Miocene of Nebraska and is represented by an anterior plastral lobe, which clearly preserves the plastral hinge (Holman and Fritz 2005). *Terrapene parornata* from the Pliocene of Oklahoma currently is hypothesized to represent the oldest recognized member of the crown-clade of *Terrapene* (Joyce et al. 2012). All other fossils of functional box turtles from North America, known from the Miocene, Pliocene, Pleistocene, and Holocene are referred to *Terrapene* at some taxonomic level.

The fossil record of *Cuora* is less extensive than that of *Terrapene*, but encompasses a similar span of time. Specimens are known from the Miocene through Holocene of Asia (Yeh 1963, Hasegawa 1980, Yeh 1985).

Testudinoidea *sensu* Testudinoidea (Joyce et al. 2004) historically was recognized to have three distinct clades, the Testudinidae (new and old world land tortoises), the Geoemydidae (Bataguridae, of some authors; old-world pond turtles and Asian box turtles), and the Emydidae (new-world pond turtles and North American box turtles). Some authors proposed to include monotypic *Platysternon megacephalum* as a testudinoid turtle, but this has been contentious (Joyce and Bell 2004, Joyce et al. 2004, Turtle Taxonomy Working Group 2010). With *Platysternon megacephalum* included, Testudinoidea contains 179 recognized species, making up 54.5% of known extant turtle diversity (Turtle Taxonomy Working Group 2010). Numerous attempts were made previously to assess the phylogeny of testudinoid turtles using morphological and molecular data (Gaffney and Meylan 1988, Shaffer et al. 1997, Krenz et al. 2005, Thomson and Shaffer 2010, Jaffe et al. 2011, Lourenço et al. 2012). Of those attempts only two attempted to sample the entirety of the taxonomic range included within Testudinoidea (Thomson and Shaffer 2010, Jaffe et al. 2011). Neither of those two analyses included morphological data, both focused instead solely on molecular data.

The paleontological record for testudinoid turtles is fairly extensive (Hay 1908, Młynarski 1976, Lapparent de Broin 2001, Claude and Tong 2004, Holman and Fritz 2005, Joyce et al. 2012). Some of that record contains fossils proposed to be potential basal members within Testudinoidea or immediately outside of it (e.g., *Mongolemys, Lindholemys*). Given the extensive fossil record and diversity within Testudinoidea, a phylogeny that includes

morphological characters is necessary to allow for the robust identification of fossils and to allow fossils to impact tree topology.

In this work, I describe the anatomy of a fossil specimen of a new functional box turtle from the Eocene-Oligocene boundary of North America, and provide a discussion of my efforts to estimate its phylogenetic relationships. Superficially, the specimen closely resembles modern *Terrapene* and modern *Cuora*, but differs in some characteristics of the shell. The specimen has a single diagnostic character of Testudinoidea. The placement of this taxon temporally and geographically and testudinoid affinities make it central to our understanding of the evolutionary history of Testudinoidea and of 'box turtles,' either as a member of an already-recognized lineage of functional box turtles, or as indicating yet another of box-turtle anatomy within Cryptodira.

GEOLOGIC SETTING

The specimen described here was collected from Rifle Range Hollow (TMM locality 40688) located within the Vieja Formation of west Texas. Original collections of fossils from the Vieja Formation were made by J. Willis Stovall of the University of Oklahoma (OU) in 1946 (Stovall 1948). Subsequent material was collected by Jack Wilson of The University of Texas at Austin (UT-Austin) in the 1960s (Wilson 1966, Wilson 1977). The mammalian fauna of Rifle Range Hollow is recognized as belonging to the Por Venir local fauna (Wilson 1977). The Por Venir local fauna is contained within an unnamed section that is bracketed by two different radioisotopically dated sections. The base of the unnamed section is the Chambers Tuff that is potassium-argon dated at 38.6 +/- 1.2 million years ago (MYA). The unnamed section is constrained at the upper limit by the Bracks Rhyolite, which is potassium-argon dated at 36.5 +/-

1.2 MYA (Wilson 1977). The dates associated with this formation were made many decades ago and may benefit from finer resolution argon-argon dating, but they do constrain the Por Venir local fauna, and place the fauna within the currently understood temporal extent of the Chadronian land mammal age. The Chadronian spans the Eocene/Oligocene boundary in North America (Prothero and Emery 2004).

METHODS

The specimen described here is TMM 40688-93 and was collected by John Kalb in 2006 from Rifle Range Hollow. It is housed at the Vertebrate Paleontology Laboratory at UT-Austin. It is three-dimensionally preserved in a hard, dark red, hematite stone, which encased the specimen and formed a hard nodule around it. Nodular encasement of specimens is common from Rifle Range Hollow and was noted by Wilson (1977). The bone of the specimen is partially replaced with hematite, and hematite is observable in the pores of the bone. A large portion of the shell remains intact and the plastron is in place. Only the posterior portion of the specimen is visible; the anterior portion of the shell still is covered by matrix. Initial collection of the specimen resulted in multiple pieces being removed from the exterior of the carapace. Much of what is visible on the main block containing the specimen is only a small skin of bone a few millimeters thick. The interior of the shell was filled with sediment that appears homogenous with the matrix covering the outer portion of the turtle. Mechanical preparation of the specimen, particularly to expose the interior portion of the shell and any elements inside, was not undertaken; preparation would likely have damaged the remaining layer of thin carapacial bone, due to the hard nature of the matrix and the small amount of bone still present.

As an alternative to potentially destructive mechanical preparation the specimen was scanned using x-ray computed tomography (XRCT) at The University of Texas at Austin High Resolution X-Ray Computed Tomography Center (UTCT). A high output x-ray source was used with 450 kV. The detector used in the scan has a 1024 x 1024 pixel area. Scans were taken in 1400 views with one sample per view; the field of view was 152.2342 mm with an interslice spacing of 0.25 mm, resulting in 726 slices through the specimen. I performed the digital preparation of the resultant dataset using VGStudioMax 2.1. TMM 40688-93 is described both from physical and digital data. The digital data are housed with the specimen and archived at: www.digimorph.org/specimens/Viejaemys_bellicosus

The nature of the matrix and preservation of the specimen did not allow for perfect clarity in the XRCT data. The radiodensity differences between bone and matrix in an ideal dataset are high so that bone is easily discerned from matrix. Unfortunately in the case of TMM 40688-93 the radiodensity difference between the bone and the matrix is small. This is a reflection of the small amount of bone still present and the infilling of the shell with matrix of the same type that covers the specimen. The low difference in radiodensity made the specimen difficult to digitally process, and not all morphological features that are potentially preserved within the specimen are readily seen in the XRCT scan.

To assess the phylogenetic placement of the new taxon, a dataset of testudinoid turtles was constructed. This dataset consists of 179 morphological characters (8 girdle characters, 14 limb characters, 50 head characters, and 106 shell characters), 9205 base pairs of molecular data, and 69 taxa. From morphological characters 125 are parsimony informative, from molecular characters 1251 are parsimony informative. The percent missing data of the matrix is 49.4%. A list of specimens examined in the construction of this dataset is provided in Appendix 1. A list of

molecular sequences used with Genbank accession numbers is provided in Appendix 2. Morphological characters for this dataset were drawn from the literature and a complete list of characters, their states, and their original sources is provided in Appendix 3. The complete scored matrices used in this analysis are provided in Nexus format in Appendix 4.

Taxonomic sampling was limited largely by the availability of specimens for the assessment of morphological data. In as many cases as possible, multiple specimens were evaluated and polymorphic (ambiguous) coding for morphological characters was used for phylogenetic reconstruction. Polymorphic coding was used in order to capture the known variation present in species testudinoid turtles (Joyce and Bell 2004, Burroughs et al. 2013).

Multiple methods have been proposed for handling polymorphisms in a morphological dataset (e.g., majority scoring, frequency scoring, and ambiguous scoring); (Wiens 1995, Wiens 1999, Stephens and Wiens 2008). However, ambiguous coding for polymorphic characters is commonly used. Ambiguous coding renders polymorphic characters phylogenetically uninformative for taxa in which they are polymorphic (i.e., they are treated as equivalents to not-applicable or missing data). There has been some debate about the propriety of ambiguous scoring, but the current consensus is that the biggest drawback of ambiguous scoring is a loss in topological resolution (Wiens 1995). A loss in resolution (i.e., a polytomy) is however, preferable to a false signal that may result in a fully resolved tree that does not reflect actual relationships (Brown and Slater 2012).

Outgroup selection for testudinoid turtles is also problematic. Some authors (e.g., Joyce and Bell 2004) argued that *Platysternon megacephalum* maybe a member of the ingroup, and. therefore, should not be used as an outgroup for all testudinoids. A Kinosternidae + Chelydridae clade has also been proposed to be the sister-taxon of the clade (e.g., Shaffer et al. 1997, Krenz et

al. 2005, and Lourenço et al. 2012). There are issues associated with selecting a kinosternid species as an outgroup, which are mostly morphological. Many of the common species of Kinosternidae have convergently evolved features shared with testudinoids such as plastral kinesis and skull features involved with feeding behaviors. Further, the plastra of kinosternid taxa lack entoplastra and have altered scute homologies (Hutchison 1991); thus making the scoring of plastral characters difficult to impossible. The selection of a chelydrid species as an outgroup also may not allow for the polarization of characters owing to the highly derived nature of snapping turtles. Initially a single outgroup was chosen (*Chelydra serpentina*), but after conducting analyses, my results did not firmly establish the location of this fossil. To test whether lack of resolution was driven by outgroup selection, I added three more outgroups that might be expected to affect placement of the fossil based on morphological characters. In those analyses the four outgroups that were used were *Chelydra serpentina, Macrochelys temminckii, Caretta caretta,* and *Apalone spinfera*.

Molecular data included two nuclear genes, recombination activating gene 1 (RAG1), and recombination activating gene 2 (RAG2), and one mitochondrial gene NADH dehydrogenase subunit 4 (ND4). Molecular sequences for this analysis were drawn from Genbank. They were downloaded as FASTA files and aligned using Fast Statistical Alignment (FSA; Bradley et al. 2009). Aligned sequences were concatenated in Mesquite 2.75 (Maddison and Maddison 2011). The taxonomic sampling for molecular data largely overlaps with the morphological sampling. There are three species represented by fossils which lack molecular data (TMM 40688-93, *Terrapene corneri*, and *Terrapene parornata*). Six extant species (*Pseudemys catespilla*, *Morenia petersi*, *Notochelys platynota*, *Cyclemys tcheponensis*, *Cuora mccordi*, and *Cuora aurocapitata*), also do not have molecular data. Not all specimens had

complete molecular sampling, but each dataset had a degree of overlap such that using at least two of the three genes could generate a complete set of taxonomic sampling.

Phylogenetic analyses were reconstructed using parsimony, maximum likelihood, and Bayesian methods. Parsimony analyses were run using PAUP* 4.0B10 (Swofford 2003). Maximum likelihood estimates were constructed using Garli 2.0 (Zwickl 2006). Bayesian phylogenetic estimates were conducted using MrBayes 3.2.1 (Ronquist and Huelsenbeck 2003). All resulting phylogenetic trees were analyzed in Mesquite 2.75 (Maddison and Maddison 2011).

Model selection for molecular sequences was performed using Mr. ModelTest 2.3 (Nylander 2008). The preferred model for both RAG1 and ND4 was GTR + I + G. The preferred model for RAG2 was HKY + G. For morphological data in maximum-likelihood and Bayesian analyses, I implemented the MK model published by Lewis (2001).

All parsimony searches were performed as heuristic searches, with random sequence addition, 1,000 replicates, and branches were swapped using the tree bisecting reconnection (TBR) method. Minimum branch lengths equal to zero were collapsed. All maximum likelihood analyses were run with 20 search replicates. The trees presented here are the best trees (those with the highest log-likelihood values). Bayesian analyses each had two runs of 2.0×10^7 generations, the first 2.0×10^6 generations were discarded as burn-in. Convergence was assessed using the SumP feature of MrBayes, and was visually confirmed utilizing Tracer v1.4 (Rambaut and Drummond 2007). Each gene and the morphological dataset were separated into individual partitions, with their appropriate models specified in maximum likelihood and Bayesian analyses.

All molecular datasets represent species-level exemplars. In the cases where molecular data and morphological data were combined, species level exemplars also were used. In those

cases where multiple specimens were scored for morphological data, the scorings were combined in Mesquite (using concatenate Matrix command), into a single species-level terminal. I also ran a single specimen-level morphological analysis without polymorphic coding to evaluate if multiple specimens of the same species clustered together.

Systematic Paleontology

Testudines Linnaeus, 1758 sensu *Testudines* Joyce et al. 2004

Cryptodira Cope, 1868 sensu *Cryptodira* Joyce et al. 2004

TMM 40688-93 gen. et. sp. nov.

Diagnosis – The specimen is referred to Cryptodira based upon the presence of shell morphology that is consistent with retracting the neck inside of the shell. TMM 40688-93 is distinct from all cryptodires by having plastral kinesis consistent with functional box turtle anatomy, making it distinct from all turtles which are not functional box turtles. With respect to known functional box turtles TMM 40688-93 is also distinct. TMM 40688-93 is distinct from *Planetochelys* by having costals that are curved posteriorly at the proximal and distal ends, similar to those seen in extant emydids. *Planetochelys* has interlocking wedge shaped costals that do not curve, which are similar to those seen in extant tortoises (Weems 1988). TMM 40688-93 is distinct from *Ptychogaster* by having the presence of a costiform process. The phylogenetic analyses performed for this study support a distinct set of characters for the turtle. TMM 40688-93 lacks flaring of the posterior margins (character 57 state 0), has a single plastral hinge (character 58 state 1), and has the presence of a costiform process (character 179 state 1). States

for characters 57 and 179 make the turtle distinct from all other turtles with a plastral hinge in this analysis (e.g., specimens of *Terrapene* and *Cuora*).

Holotype – TMM 40688-63, a nearly complete carapace and plastron with scapulae, humeri, a left femur, a pubis, and an illium preserved within the shell. Additional material of the shell (costals and peripherals) is preserved in eight additional pieces. Seven of the pieces were not included in the XRCT scan nor have they been mechanically prepared.

Locality and Horizon - Rifle Range Hollow (TMM locality 40688), Presidio County, Texas; Vieja Formation, latest Eocene/earliest Oligocene.

DESCRIPTION

Shell – The holotype shell of the new taxon is shown in Figure 1. The XRCT scan reveals that the anterior portion of the carapace is slightly crushed, where it is pushed down and moved medially (Figure 2). The carapace is domed. The dorsalmost section of the carpace is relatively round and does not appear flattened on the top. The highest section of the shell is inferred to be just posterior to the antero-posterior midline when viewed laterally (Figure 3). The eight additional pieces preserve the bulk of the thickness of the carapacial bones (Figures 4-11).

In dorsal view the carapace is approximately oval in shape. The posterior peripherals of the shell are not flared outward as seen in many extant testudinoids.

The lateral view of the XRCT scan of the new taxon (Figure 3) shows the anterior margin of the carapace is straight and lacks an anterior-dorsal inclination. The slight crushing of the specimen may distort this character slightly; although an offset in lateral peripherals is not seen.

Nuchal – The nuchal of the new taxon is visible only in the XRCT scan (Figures 12 and 13). The nuchal is 25 mm long along the mid-line (anterior-posterior), and the preserved portion is 30 mm wide at its widest point, approximately halfway along the anterior-posterior length. In dorsal view, the left lateral edge of the nuchal appears to be broken; the right lateral section preserves a costiform process.

Neurals – Eight neurals are preserved in the new taxon. Following the neural numbering scheme of Zangerl (1969), in which counts begin with the midline element that is immediately posterior of the nuchal as representative of the first neural, moving posterior neurals are numbered sequentially, until an elemental lacking a vertebral centrum is reached; the first neural is visible only in the XRCT scan (Figures 14 and 15). The remaining seven neurals are visible on the exposed dorsal surface of the shell (Figure 16). Data on neural configuration are based on the number of other bones that contact a neural in the carapace. A neural with a square configuration contacts four bones and has four edges, one with a pentagonal configuration contacts five bones and has five edges, etc. (for review see Burroughs et al. 2013). The anterior to posterior sequential configurations of the neurals for the new taxon are square-hexagonal-square-hexagonal-hexagonal-hexagonal-hexagonal-pentagonal. The remains of a mid-dorsal keel are present on neurals 2-7 (Figure 16, inset). On neurals 3, 4, and 5 a small tubercle is present in the center of the neural. These tubercles also may be observed on some specimens of *Terrapene*, and are strongly associated with the presence of a mid-dorsal keel.

Costals – Eight sets of costals are present in the new taxon. The proximal ends of the first and second costals are visible only in the XRCT scan (Figure 15). The posterior half of the third costal and the remaining costals are exposed on the surface of the shell. Each costal has a continuous width along its length, with a long rib tip that inserts into the adjacent peripheral. The

overall width and overall length decrease posteriorly. The proximal ends of the eighth costals partially meet at the midline. The anterior portion of each proximal end contacts the posterior portion of the eighth neural. The remaining section of the proximal ends of each costal meet along the midline and frame the first suprapygal (Figure 17).

Peripherals and Pygal region – The total number of peripherals is unknown, because the anterior peripherals are not discernible. The medial portion of the bridge peripherals is missing, but the lateral edges are visible in ventral view (Figure 18). Based on the preservation of the lateral edges of the peripherals, I infer that a bridge was reduced or absent, as seen in *Cuora* and *Terrapene*.

The peripherals on the left side of the specimen are exposed on its dorsal surface. They are wider than long, and consistent in shape and size with peripherals seen posterior of the bridge in extant emydids. There are two unpaired suprapygals present at the midline. The first has a triangular shape with the apex pointing anterodorsally. It is framed along its anterior edges by the eighth costals (Figure 17). The posterior suprapygal is shaped like an inverted triangle or spade with the point facing posteroventrally. The peripherals adjacent to it are broken and pushed upwards (dorsally), obscuring most of the pygal and the lowest portion of the second suprapygal. If these peripherals were in their natural position this would show that the posterior lobe of the plastron would be fully enclosed by the peripherals.

Carapacial scutes – In lateral view of a shaded XRCT image (Figure 19), portions of the first, second, and third left pleural scutes and a few of the marginal scutes are preserved. The shape of the second pleural and the marginals are consistent with those seen in extant testudinoids.

Plastron – As seen in other functional box turtles (e.g., *Cuora*, *Planetochelys*, and *Terrapene*) the plastron is separated into two distinct lobes. The anterior lobe contains the epiplastra, the entoplastron, and hyoplastra. The posterior lobe contains the hypoplastra and xiphiplastra; there is no mesoplastron. A well-developed plastral hinge is along the hyoplastron-hypoplastron suture, and separates the two lobes. The anterior lobe is narrower than the posterior lobe and fits into a groove that can be seen in the XRCT scan image of the posterior lobe (Figure 20), although sediment fills the space between the two lobes.

The anterior lobe of the plastron is visibly broken in two places. The anterior section of the plastron, where the epiplastra meet at the midline, is broken (Figure 21). Along the lateral edge of the left epiplastron and hyoplastron there is a second break. Digital disarticulation of the anterior lobe reveals some of the morphology of the bones. Although both epiplastra are broken, they have a trapezoidal shape similar to that of extant testudinoids. The entoplastron is elongate with a maximum length longer than its maximum width. The maximum width is near the posterior end. The hyoplastra are narrower than the hypoplastra. The left hyoplastron is broken, revealing part of the buttress dorsally.

The posterior lobe of the plastron is wider than the anterior lobe and is rounded posteriorly. The posterior rounding is seen in other functional box turtles and is consistent with the ability of the turtle to fully close the posterior lobe tightly against the interior edge of the carapace. Digital preparation of the hypoplastra did not reveal any preserved elements of the posterior buttresses. The scan does reveal a long medial ridge along the dorsal midline, with internal concavities lateral to the ridge on the posterior lobe (Figure 22).

The plastral scutes are preserved as impressions in the surrounding matrix (Figure 23). The left gular scute was rounded anteriorly. The length of the inter-gular seam is 18.7 mm. Both right and left humeral are curved anteriorly along the humeral-gular seam. Posteriorly, they are straight along the humeral-pectoral seam, and slightly offset where they meet at the midline. The length of the inter-humeral seam is 22.3 mm. The pectorals are short and rectangular. The pectoral-abdominal seam is straight and coincides with the hyo-hypoplastral seam along which the plastral hinge is formed, such that the pectoral and abdominal scutes do not overlap the plastral hinge, but meet along its boundary. The length of the inter-pectoral seam is 15.9 mm. The abdominal-femoral seam slopes posteromedially, such that the abdominals are longer (anterior-posterior) along the midline than they are laterally. The length of the inter-abdominal seam is 31.7 mm. The femoral scutes are narrow at the midline and widen considerably at the lateral edges. The length of the inter-fermoral seam is 10.5 mm. The femoral-anal seam is sloped anteromedially. The anals are rounded posteriorly, with no emargination or anal notch present. The length of the inter-anal seam is 32.7 mm.

Appendicular skeleton – The appendicular skeleton of turtles was described numerous times with different names for presumably homologous structures (e.g., Bojanus 1819-1821, Thomson 1932, and Walker 1973). The description of the long bones here follows the terminology used by Walker (1973) as modified by Bortolini et al. (2012).

Humeri – Both humeri are preserved in the interior portion of the shell and can be seen only in the XRCT images. The humeri are in near-life position. The left humerus is the best prepared with most of the corpus and the proximal end preserved (cranial view, Figure 24; caudal view, Figure 25). The corpus is bowed cranially with a small break just below the head and another two-thirds down the length of the corpus. The distal end is not preserved. Viewed

from the cranial aspect the cranial tuberculum is large and swept caudally. Only the medial edge of the humeral head can be seen (Figure 24.1). The caudal tuberculum is larger than the cranial tuberculum, with a broad flat shape that projects proximally and caudally.

Scapula – The right scapula is preserved. It was digitally prepared and appears unbroken (Figure 26). The coracoid is not preserved, and does not appear to have been fused with the scapula. The scapular process is longer than the acromial process and the two intersect at approximately a 90-degree angle. The glenoid fossa is not easily seen in the scan, nor is it complete, because the coracoid is missing. The portion of the glenoid that is preserved includes the process where the triceps brachii attaches.

Femur – The left femur is preserved inside the carapace and was prepared digitally. From the cranial perspective (Figure 27), the portion of the head that is visible is elongate towards the medial side. The femoral collum could not be digitally prepared. The major trochanter is large and swept caudally. There is a depression between the head and the major trochanter. The corpus of the femur is curved slightly. The minor trochanter is small and brushed almost straight back caudally; most of it is obscured by the femoral head with only the most medial portion is visible. From the caudal aspect (Figure 28), the trochanteric fossa is deep and v-shaped; the trochanters are not coalesced. The trochanteric fossa has a distinct u-shape. The fibular and tibial condyles are not particularly distinct and appear merged together.

Pelvis – The left ischium is preserved, and was prepared digitally (Figure 29). The ischium has a long body with a narrow ischial-pubic tuberculum. The acetabular end is broader, but is not well preserved. The lateral ischial process is short, wide, and blunt. The left ilium also

is present, with part of the acetablum preserved at its distal end (Figure 30). The proximal end of the ilium is not preserved. The body of the ilium is curved caudally along its length.

COMPARISON WITH EXTANT TESTUDINOID TAXA

The assignation of this new taxon to Testudinoidea warrants an osteological comparison with extant testudinoid turtles and other 'box turtles' represented by fossils (e.g., *Planetochelys, Ptychogaster*). The description above applies to TMM 40688-93. Comparisons are provided below with extant *Cuora amboinensis, Emys orbicularis, Emydoidea blandingii, Geochelone sulcata, Notochelys platynota, Pyxidea mouhotii, Terrapene carolina, Terrapene coahuila, Terrapene ornata, Testudo graeca,* and *Trachemy scripta*.

Shell - The doming of the shell of TMM 40688-93 is comparable to that of extant *Terrapene coahuila* or *Cuora amboinensis*. The doming is not as high or pronounced as in extant specimens of *Testudo graeca* or *Geochelone sulcata*. Modern specimens of *Notochelys platynota*, *Pyxidea mouhotii*, *Terrapene carolina, Terrapene ornata,* or *Terrapene nelsoni*, are all relatively flattened on the top. *Planetochelys savoei* was reconstructed with a relatively flat dorsal portion of the carapace (Weems 1988).

Flaring of the posterior peripherals is found in many extant testudinoid taxa, and was observed in *Terrapene carolina, Terrapene ornata, Cuora amboinensis*, and *Testudo graeca*. Some of the variation in the degree of flaring among testudinoids was documented by Joyce and Bell (2004). The posterior peripherals of unpublished specimens examined at UCMP of *Planetochelys* spp. do not flare, and the figure of the holotype of *Planetochelys savoei* does not show any flaring (Weems 1988). A line-drawing reconstruction of *Ptychogaster batelleri* does not indicate flaring of the posterior peripherals in that taxon (Hervet 2003).

The lateral view of TMM 40688-93 lacks a dorsal inclination of the anterior peripherals. In lateral view of specimens of *Terrapene* and *Cuora* (Figures 31 and 32), the anterior margin of the portion of the carapace that is anterior to the bridge (usually made up of peripherals 1-5) exhibits a steep antero-dorsal inclination. This inclination is not seen to the same degree in *Emys orbicularis* (Figure 33) or *Emydoidea blandingii* (Figure 34). The inclination is virtually non-existent in akinetic specimens exemplified here by *Trachemys scripta* (Figure 35). The reconstruction of *Planetochelys savoei* indicates that the anterior section of the carapace would have had an inclination similar to that seen in *Emys orbicularis*, although it appears to be based solely on artistic license, because the anterior portion of the shell of the taxon is not preserved. To date the anterior peripherals are not preserved in articulation of specimens of *Planetochelys* spp. Specimens of *Ptychogaster* spp. often do not have the anterior peripherals preserved; because reconstructions of *Ptychogaster* are shown in dorsal or ventral view and not in lateral view, the condition of the anterior edge is unknown. With the slight crushing present, it is possible that TMM 40688-93 may have had an inclination similar to that seen in *Emys orbicularis* or *Notochelys platynota,* but not as steep as that seen in *Emydoidea*, *Terrapene*, or *Cuora*.

Nuchal - Costiform processes are not present in *Emys orbicularis*, *Emydoidea blandingii*, *Testudo graeca, Terrapene* spp., *Cuora* spp., or in reconstructions or figured images of *Ptychogaster*. Costiform processes were observed in a specimen of *Planetochelys* (personal observation, UCMP 120000) and were described as being present in *Planetochelys* (Hutchison 2003). The nuchals of *Emys orbicularis*, *Emydoidea blandingii*, *Terrapene coahuila*, and *Pyxidea mouhotii* are trapezoidal in shape with the widest portion being approximately a third of the way along the antero-posterior length of the nuchal.

Neurals – The tubercles preserved on some of the neurals in the new taxon, are similar to those observed in extant *Terrapene carolina* (e.g., CAS 228375) and other testudinoids with mid-dorsal keels (for review see Joyce and Bell 2004).

Costals - The costals are shaped like those seen in extant Emydids and *Cuora* and are unlike extant tortoises or *Planetochelys* (e.g., interlocking wedge shapes).

Carapacial scutes –The shape of the first and second pleural, and marginal scute impressions are consistent in general shape with those seen in *Terrapene*, *Cuora*, *Emydoidea*, *Emys*, *Testudo*, and *Notochelys*.

Plastron – A groove along the dorsal surface of the plastral hinge similar to that seen in *Cuora*, *Terrapene,* and *Emydoidea*, here exemplified by *Terrapene coahuila* (Figure 36) appears to be present in the XRCT scan image of the posterior lobe (Figure 20).

Anterior lobe - The entoplastron of TMM 40688-93 is relatively more elongate than those of *Cuora, Terrapene*, or *Planetochelys*. Extant and fossil *Terrapene* and extant *Cuora* (Figure 37) have maximum widths near the anterior edge of the plastron and come to a point, with the tip pointing posteriorly, when viewed ventrally.

The buttress seen in the new taxon is larger and more robust than that seen in *Terrapene* or *Cuora*, but not as robust as that seen in *Emys orbicularis* or *Emydoidea blandingii*.

Posterior lobe – The scan does reveal that there is a long medial ridge, with internal concavities lateral to the ridge, on the posterior lobe (Figure 22). This is seen in many specimens of *Terrapene* (Figure 38). The ridge is not seen in *Cuora amboinensis* although there is a rise

along the mid-line of the posterior lobe. In *Cuora* the rise is manifested as a series of tubercles, rather than a single ridge.

Humeri - A cranially bowed corpus is seen in *Cuora*, *Testudo, Notochelys*, *Terrapene, Emys,* and *Emydoidea* in addition to the new taxon. Viewed from the cranial aspect the cranial tuberculum of the new taxon is large and swept caudally, similar to that seen in *Emys orbicularis*, *Emydoidea blandingii*, and *Terrapene carolina*. The partially preserved medial edge of the head shows a similar condition to the medial edge seen in *Emys orbicularis* and *Emydoidea blandingii*, but not seen in *Terrapene carolina* (Figures 39-41). The caudal tuberculum projects proximally and is similar to that seen in *Emys*, *Emydiodea*, and *Terrapene*.

Scapula –The 90-degree angle of the scapular process, is found in modern *Emys orbicularis*, *Terrapene carolina*, and *Pxyidea mouhotii*. The angle is less in extant *Testudo graeca*, *Geochelone sulcata*, and *Notochelys platynota*.

Femur –The major trochanter of TMM 40688-93 is larger and not brushed as far caudally as seen in extant *Terrapene carolina* (Figure 42) or *Emydoidea blandingii* (Figure 43). The major trochanter also is larger than that seen in *Emys orbicularis* (Figure 44). The depression between the head and the major trochanter is similar to that seen in *Emys orbicularis* and *Emydoidea blandingii*. The corpus of the femur of the holotype specimen is curved slightly, but not to the degree seen in *Terrapene*, *Emys*, or *Emydoidea*. In extant testudinids (*Geochelone sulcata* and *Testudo graeca*) the corpus of the femur is curved slightly and is similar to the condition seen in *Cuora amboinensis* and *Notochelys platynota*. The femoral head in TMM 40688-93 obscures a large portion of the minor trochanter and this is similar to the conditions

observed for *Testudo graeca*, *Geochelone sulcata*, *Terrapene*, and *Emydoidea blandingii*. The minor trochanter is not as obscured by the head in *Emys orbicularis* or *Cuora amboinensis*.

The trochanteric fossa is similar in shape and depth to those of *Emys* and *Emydoidea* with a distinct depth and u-shape (Figures 45 and 46). The fossa seen in *Terrapene carolina* is shallower with a v-shape (Figure 47). In *Testudo graeca* and *Geochelone sulcata* the trochanteric fossa is reduced to a small depression with limited depth. The fibular and tibial condyles are not particularly distinct in TMM 40688-93, the merging or fusion of the condyles previously was proposed as a characteristic common to *Terrapene* and *Cuora* (Bramble 1974). However, observed specimens of *Testudo graeca*, *Geochelone sulcata, and Pyxidea mouhotii*, also have merged or fused condyles of the distal end of the femur.

Pelvis –The lateral ischial process of TMM 40688-93 is short, wide, and blunt, particularly when compared to the narrowed point that is present in *Emydoidea blandingii* and *Terrapene ornata* (Figure 48 and Figure 49). The blunt and wide portion of the pelvis in the new taxon is similar to that seen in *Geochelone sulcata*. The body of the ilium is curved caudally along its length in the new taxon; that condition is present in virtually all turtles, and is exemplified here by *Emydoidea blandingii* (Figure 50).

PHYLOGENETIC ANALYSES

Results from parsimony, maximum-likelihood, and Bayesian analyses are summarized in Table 1. In each case, I assessed the placement of the new taxon and monophyly of Testudinidae, Geoemydidae, Emydidae, and two traditionally recognized sub-clades within the Emydidae, the Emydinae and the Deirochelyinae. Additionally, the monophyly of genera represented by multiple species was assessed. Results discussed below, will be focused on the hypotheses

generated using all three molecular genes and morphological data combined into species-level analyses and between specimen-level and species-level morphological analyses constructed in a Bayesian framework.

The strict-consensus of 10,000 most parsimonious trees, from analysis of the combined morphological and molecular dataset is shown in Figure 51. A basal polytomy formed by most of the ingroup taxa is illustrated and indicates no resolution among ingroup taxa. TMM 40688-93 falls into the large basal polytomy and its relationship to all other taxa is unresolved. Four clades are recovered. Three species of *Cuora* form a clade, all of the species included in the genus *Cyclemys* form a clade, and four other taxa, *Malayemys subtrijuga*, *Glyptemys insculpta*, *Graptemys geographica*, and *Platysternon megacephalum*, form a clade. Among the three traditionally recognized clades within Testudinoidea, only the Testudinidae is recovered as monophyletic, which includes the genera *Geochelone, Manouria Testudo, Indotestudo, Dipsochelys*, and *Gopherus*.

A 50% majority-rules consensus of the 10,000 most parsimonious trees is shown in Figure 52. This is tree is almost completely dichotomously branching, with only two polytomies shown. One polytomy is between a clade including *Graptemys kohni* + *Graptemys nigrinoda* + *Malaclemmys terrapin* and the remaining traditionally recognize deirochelyine taxa: *Pseudemys, Trachemys, Graptemys pseudogeographica*, *Chrysemys,* and *Deirochelys.* The second polytomy is formed by two major clades containing most of the geoemydid taxa formed into a polytomy with *Rhinoclemmys pulcherrima*. The Deirochelyinae is shown as monophyletic. A clade that contains *Terrapene* and TMM 40688-93 is supported, but emydine monophyly is not recovered. A monophyletic Testudinidae with *Dipsochelys, Gopherus, Geochelone, Indotestudo, Testudo,* and *Manouria* are all shown as a clade. *Morenia petersi*, a traditionally recognized geoemydid

taxon, is the immediate sister taxon to the rest of Testudinidae. The remainder of the Geoemydidae is supported as monophyletic, as well as a clade containing *Cuora* and *Pyxidea*.

From maximum-likelihood analyses, the best tree recovered had a log likelihood of -23250.94; the topology is shown in Figure 53. That analysis recovered *Deirochelys reticularia* as the basal-most member of the ingroup and did not recover a monophyletic Deirochelyinae. A monophyletic Emydinae was recovered. A monophyletic clade formed of *Terrapene* and TMM 40668-93 was recovered within the Emydinae. Emydinae is the immediate sister to a clade formed by Testudinidae + Geoemydidae. A monophyletic Testudinidae is recovered and includes three separate clades, a *Gopherus* clade, a *Geochelone* + *Dipsochelys* clade, and a *Indotestudo* + *Testudo* clade. Geoemydidae is not recovered as monophyletic, but only due to the placement of *Morenia petersi* within the Deirochelyinae. Otherwise, all traditionally recognized geoemydid taxa are recovered in a single monophyletic clade. Contained within that clade, are three clades. A clade of all species of *Cuora* and *Pyxidea*, a clade of all species *Cyclemys*, and a clade of all species of *Rhinoclemmys* are recovered within the Geoemydidae. The clade of *Rhinoclemmys* was not recovered in either parsimony analysis.

The resulting tree topology from combined molecular and morphological dataset using a Bayesian framework is shown in Figure 54. A basal polytomy was recovered in that analysis, and none of the major clades were fully recovered as monophyletic. Taxa considered to belong to the Emydinae were not recovered together for the most part. A clade containing *Emys, Emydoidea blandingii*, *Terrapene,* and TMM 40688-93 was recovered. However, *Terrapene* was not recovered as monophyletic; *Terrapene corneri* forms part of the basal polytomy. Taxa traditionally recognized as deirochelyines were found mostly in the basal polytomy. One clade of mostly Deirochelyine taxa was recovered containing *Pseudemys texana, Chrysemys picta,*

Trachemys scripta, Graptemys kohni, Graptemys nigrinoda, *Malaclemmys terrapin,* but that clade also contained the geoemydid *Morenia petersi*. The remaining geoemydid taxa were recovered in five separate clades branching from the basal polytomy. The Testudinidae was not recovered as monophyletic, but was grouped into two clades branching from the basal polytomy.

Figure 55 illustrates the tree topology with specimen-level terminals generated in a Bayesian framework using only morphological characters. TMM 40688-93 is shown in a clade that is formed of functional box turtles, including taxa of *Terrapene* and *Cuora*. The topology shows a monophyletic Testudinidae, but all other traditionally recognized testudinoid taxa are not shown as monophyletic. This includes all genera represented by multiple species. Only three species with multiple specimens scored were recovered as monophyletic, *Terrapene coahuila*, *Testudo kleinmanni,* and *Rhinoclemmys funerea*. The morphology-only species-level Bayesian tree is shown in Figure 56. In that tree, TMM 40688-93 is recovered as the sister taxon to *Terrapene ornata*. The tree also shows a monophyletic Testudinidae as found in the previous tree, it and further shares three other clades with the specimen-level tree. A clade containing *Cuora mccordi, Cuora pani, Cuora aurocapitata,* and *Cuora zhoui* is shown; a clade containing *Emys orbicularis, Emys trinacris*, and *Emydoidea blandingii* is shown (this clade was partially recovered in the specimen-level analysis), and a clade containing *Malaclemmys terrapin* and *Graptemys kohni* is also shown.

In parsimony and Bayesian analyses of combined data with four outgroups (Figures 57 and 58), the resolution is similar to those analyses with only *Chelydra* as an outgroup. However, the position of *Chelydra serpentina* itself is distinct from other analyses with *Chelydra* nested within the ingroup instead of nesting lower in the tree as an outgroup.

The fossil representing *Terrapene parornata* is consistently recovered as a member of *Terrapene*, however it is not consistently recovered as being more closely related to *Terrapene ornata* and *Terrapene nelsoni* as proposed by Joyce et al. (2012). Recent population genetic work on *Terrapene* indicated that the genetic recognition of species in *Terrapene* is problematic (Martin et al. 2013). Further, work on *Terrapene* evaluating variation and morphological distinction between species, in both the present and the Pleistocene, further documented that purportedly useful characters for morphological diagnoses are still problematic (Vitek and Burroughs 2012). The position of *Terrapene corneri* in my analyses calls into question the validity of the taxon; this echoes the sentiments of Joyce et al. (2012). *Terrapene corneri* is a taxonomic equivalent of *Terrapene nelsoni* and at least two specimens of *Terrapene ornata* in my analysis. As a result, the taxon lacks an apomorphic diagnosis and is of questionable validity. Visual inspection of *Terrapene corneri* does reveal that its morphology is markedly different than *Terrapene nelsoni* or *Terrapene ornata* in some characteristics. These characters have not been discretized for inclusion in phylogenetic analysis, nor evaluated for intraspecific variation within any of the relevant taxa.

DISCUSSION

The resulting hypotheses from multiple phylogenetic estimations from this study support a relationship between TMM 40688-93 and *Terrapene* (Figures 52, 53, 54, 57, and 58). If TMM 40668-93 is closely relate to *Terrapene* the implications for the evolutionary history of *Terrapene* would be large. The divergence of *Terrapene* would be pushed back to the Oligocene, when previously hypothesized to occur in the Miocene (Milstead 1969). Further, some analyses recover *Terrapene* as the most derived taxon within the Emydinae, indicating earlier splits

between other taxa contained within the Emydidae (Gaffney and Meylan 1988, Shaffer et al. 1997, Wiens et al. 2010). If this is in fact the case and TMM 40688-93 is closely related to *Terrapene* this would push the divergences of many other taxa back into the earliest Oligocene or even earlier into the Eocene. These results are not inconsistent with those of Claude and Tong (2004), who used morphology to suggest Eocene divergences for modern taxa, and molecular clock dating places the divergence of crown lineages of Testudinoidea in the Paleogene (Lourenço et al. 2012). All of this is dependent on if TMM 40688-93 represents a basal member of *Terrapene*.

Phylogenetic analyses from this study indicate TMM 40688-93 has a unique set of characters with respect to all testudinoid taxa included. TMM 40688-93 also has the single applicable character for diagnosing the turtle to Testudinoidea, absence of inframarginal scutes (character 178 state 0). Despite this, I diagnose TMM 40688-93 as a unique taxon belonging to Cryptodira, not the more inclusive Testudinoidea.

The diagnosis to Testudinoidea for this new taxon would be based on the lack of inframarginal scutes. This character was proposed as an informative character for the diagnosis of Testudinoidea by Gaffney and Meylan (1988) and was based on the presence of inframarginals in taxa assumed to be basal (or stem) testudinoids (i.e., *Mongolemys*). The problem associated with this character is that inframarginals also are not present in *Chelydra serpentina*, in all Trionychidae, and most Kinosternidae; in short in most extant cryptodires, inframarginal scutes are not present. The loss of inframarginal scutes within cryptodires is a character subject to considerable homoplasy and is thus unsuitable for an unambiguous diagnosis of Testudinoidea.

It is also not currently possible to diagnosis TMM 40688-93 as a member of one of the more inclusive clades contained in Testudinoidea (e.g., Emydidae or Geoemydidae). Homoplasy is a critical issue affecting this. The presence of the costiform process is homoplastic and is found in multiple turtles in this analysis, which are not closely (e.g., *Macrochelys temmenckii* and *Platysternon megacephalum*). Some characteristics of TMM 40688-93 are shared with or similar to characters seen in *Cuora* and *Terrapene*. But these may be tied to functional constraints involved with being a functional box turtle and thus be homoplastic (e.g., shell shape, neural configuration, plastron shape, and peripheral shape; Joyce and Bell 2004, Claude 2006, Karl and Tichy 2008, Angielczyk et al. 2010, Burroughs et al. 2013). Others are known to be variable within taxa (e.g., the flaring of the posterior peripherals, neural configuration and presence of a mid-dorsal keel) (Burroughs et al. 2013).

Variation within emydid and geoemydid taxa makes the diagnoses of either clade based on a single set of anatomical features virtually impossible (Joyce and Bell 2004). In the case of TMM 40688-93 none of the characteristics proposed by Gaffney and Meylan (1988) for the diagnosis of Emydidae or Geoemydidae are applicable for the evaluation of this taxon. A single unambiguous character proposed in the diagnosis of Testudinidae can be evaluated, the coalesence of the femoral trochanters; all other proposed characters cannot be scored. TMM 40688-93 does not have coalesced trochanters and therefore can be excluded from Testudinidae.

In addition to polymorphism, the time differential between TMM 40688-93 and extant crown-clade taxa is extensive. The divergence between Testudinoidea and other cryptodires is hypothesized to have occurred in the Late Cretaceous (Krenz et al. 2005, Lourenço et al. 2012). As a result the branches separating these taxa are extremely long. Over the length of long branches we expect character states to transform out resulting in an increase in missing data and

homoplasy. Over long branch lengths we also expect higher rate heterogeneity between anatomical and molecular regions, which may ultimately cause characters to transform out more quickly resulting in disparate estimates of phylogeny. Thus further complicating the issue of estimating phylogeny.

All of these issues (long branches, homoplasy, and polymorphism) will impact the resolution of estimates of phylogeny. This is an important issue raised by the analyses here. The monophyly of Testudinoidea has largely been accepted (e.g., McDowell 1964, Gaffney and Meylan 1988, Shaffer et al. 1997, Krenz et al. 2005, Lourenço et al. 2012), but the monophyly of the proposed clades within Testudinoidea remains poorly established (Thomson and Shaffer 2010, Jaffe et al. 2011). The analyses conducted for this study also indicate that the monophyly of clades within the Testudinoidea is not adequately established or supported.

Utilizing a combined dataset of morphological and molecular characters to reconstruct phylogeny supports the monophyly of only one of the three major clades in Testudinoidea, the Testudinidae. The loss of resolution in my analyses as compared with others is not surprising, because I used polymorphic scoring for morphological characters. In doing so I effectively reduced the number of characters available for use in tree reconstruction and, as such, I anticipated a reduction in tree resolution. However, the loss of resolution is more consistent with the reality of our understanding of relationships within Testudinoidea, because I took into account the known amount of variation within the group.

In the case of many previous analyses, smaller levels of taxonomic sampling were used in conjunction with species-level exemplars that did not code polymorphic characters (e.g., Shaffer et al. 1997, Krenz et al. 2005, and Lourenço et al. 2012). Analyses that used more complete taxonomic sampling (e.g., Thomson and Shaffer 2010, and Jaffe et al. 2011) are not necessarily

more accurate. In the case of Thomson and Shaffer, their analyses supported the combination of Testudinidae and Geoemydidae into a single clade (*sensu* Testuguria of Joyce et al. 2004), and they recovered a monophyletic Emydidae, but they noted that the internal branches for these clades are short with low node support, indicating that incongruence between molecular data may have influenced their results (Thomson and Shaffer 2010). In the case of Jaffe et al., consistent recovery of Geoemydidae was problematic and these authors chose to constrain the existence of the clade. As a result at present our understanding of the phylogeny of Testudinoidea is less complete than previously thought.

CONCLUSIONS

TMM 40688-93 represents a new taxon of morphologically distinct cryptodire turtle. It may belong to the most inclusive clade Testudinoidea based on the absence of inframarginal scutes, however this character is homoplastic with respect to non-testudinoid cryptodiran taxa. If TMM 40688-93 represents a testudinoid turtle it may be closely related to extant *Terrapene* as supported by phylogenetic analyses from this study. Its placement within some analyses as closely allied to extant *Terrapene* can have a dramatic impact on our understanding of the evolutionary history of crown-clade testudinoids. *Terrapene* are easily among the most studied extant testudinoid taxa, yet the oldest named *Terrapene*, *Terrapene corneri*, appears to have a fully-formed box turtle plastron in the middle Miocene in North America. The origin of the group still remains a mystery. However, if TMM 40688-93 represents a potential stem member of *Terrapene* then it allows for a refocus of paleontological efforts into older time periods and localities that may allow for elucidation of the mysterious origin of this and other crown clades of testudinoids.

At present, however, TMM 40688-93 is not unambiguously diagnosable to Testudinoidea or the more inclusive clades Emydidae or Geoemydidae. This is because characteristics allowing the diagnosis of fossils to Testudinoidea are dependent on homoplastic characters. Diagnosis to Emydidae or Geoemydidae remains problematic due to issues of intraspecific variation within extant members of both lineages (Joyce and Bell 2004). The results from the phylogenetic analyses of this study indicate that there are issues with establishing the monophyly of Emydidae and Geoemydidae.To handle these problems we must address the underlying issues. Namely issues involving homoplasy, polymorphism, transformed out character states and missing data due to long branches, and low taxonomic sampling.

Many characters within Testudinoidea are homoplastic. However, some anatomical regions have not been evaluated. Characters have been proposed for constructing phylogeny from the girdles, limbs, hands, feet, and vertebrae of turtles in the past, but have remained mostly unused for decades (White 1929, Auffenberg 1961). For example the long bones and girdles found within TMM 40688-93, prompted comparison of the long bones and girdles of a variety of testudinoid taxa. That effort revealed that, particularly in functional box turtles, there are characteristics of the long bones that are not shared between *Cuora* and *Terrapene*; these characters were not included in the phylogenetic analyses conducted here, however. Disarticulated cranial elements have not been evaluated in turtles and have been noted to be useful in squamate reptiles, which have high degrees of homoplasy and polymorphism in many anatomical regions (Bell and Mead In Press). All of these areas are ripe for re-evaluation and new study, with the caveat that intraspecific variation must be accounted for.

To begin to evaluate variation, organism-wide studies must be conducted, by evaluating as many specimens of a given species as is possible. Some analyses have already been done for

some of Testudinoidea (e.g., Joyce and Bell 2004, Bever 2006, Vitek and Burroughs 2012, and Burroughs et al. 2013), but these represent only the beginning of in-depth exploration.

The bulk of these issues will be address by using larger taxonomic samples. The decisions by previous workers to utilize a small taxonomic sample, across the clade which has the most extant diversity for turtles within it, has resulted in false confidence in the monophyly of the group, because it has reduced the complexity of the relationships within Testudinoidea to being represented only by a few, divergent, end members. Future analyses evaluating the monophyly of Testudinoidea must include extant taxa that are closely related to the group and, ideally, basal and stem members of Testudinoidea represented by fossils. This study provides a minimal taxonomic sample that must be expanded upon in order to evaluate those outgroups.

By adding fossils we will begin to break up long branches that may result in transformed out character states and missing data. However, in order to adequately use fossils for phylogenetic analysis we must have confidence in their placement as basal or stem taxa. If fossils cannot be confidently placed within a tree, their value for resolving the evolutionary relationships and even their value in elucidating evolutionary phenomena is limited. As a result issues associated with homoplasy and polymorphism must be address simultaneously with increased taxonomic sampling.

Testudinoidea is a group that represents over half of extant turtle diversity. As a result the group has a long and complex evolutionary history. To elucidate the evolutionary history of this group we must coalesce multiple sources of information. The combination of molecular data, morphological data, with a large taxonomic sample will not fully elucidate this history. This is shown by the phylogenetic analyses from this study. We must combine data, have a large taxonomic sample (to include fossils), and deal with issues of homoplasy, polymorphism, and

long branches to adequately evaluate the history of Testudinoidea. Undoubtedly, as this complex history is elucidated, TMM 40688-93 will play a role in improving our understanding of the evolutionary history of testudinoid box turtles and Testudinoidea as a whole.

ACKNOWLEDGMENTS

I am greatly indebted to Drs. Chris Bell, Julia Clarke, Travis LaDuc, Patricia Holroyd, J. Howard Hutchison, and Walter Joyce for their conversations regarding turtle evolution, anatomy, and methodological and philosophical approaches to this work, as well as their careful review of my words. I thank Natasha Vitek, Zachary Morris, Joshua Lively, Will Gelnaw, Alicia Kennedy, Travis Wicks, Rachel Simon, Adam Marsh, and Michelle Stocker for numerous conversations in support of this work. I also extend my thanks to the collections managers that facilitated access to many specimens through either visitation or loans, without their efforts this work would never have been finished. I thank John Kalb for collecting the fossil described here. Chris Bell directed my attention to the existence of the fossil and paid for the XRCT scan of the specimen. I thank Jeesica Maisano and Matthew Colbert of UTCT for their work scanning and helping me learn how to digitally prepare the specimen. Finally, I thank Catherine Burroughs for her tireless and unwavering support.

Table 1a (Contained on next page): Summary of the tree topologies recovered from parsimony and maximum likelihood analyses, addressing the monophyly of Testudinidae, Bataguridae/Geoemydidae, Emydidae, the two emydid sub-clades, Emydinae, and Deirochelyinae, and noting if any of the genera represented by multiple species were recovered as monophyletic.

Analysis	Monophyly of Testudinidae	Monophyly of Bataguridae	Monophyly of Emydidae	Monophly of Emydinae	Monophyly of Deirochelyinae	Monophyly of genera with multiple species represented (each is noted)
Parsimony						
Specimen level morphology	Yes	No	No	No	No	None
Species level morphology	Yes	No	No	No	No	*Cyclemmys*
ND4 + RAG1	No	No	No	No	No	None
ND4 + RAG2	Yes	Yes	No	No	No	None
ND4 + RAG1 + RAG2	No	No	No	No	No	None
RAG1 + RAG2	Yes	No	No	No	No	None
Species level morphology + ND4 + RAG1 + RAG2	Yes	No	No	No	No	*Cyclemmys, Geochelone + Dipsochelys, Gopherus*
Maximum Likelihood						
Specimen level morphology	Yes	No	No	No	No	None
Species level morphology	Yes	No	No	No	No	*Cyclemmys*
ND4 + RAG1	No	No	No	No	No	None
ND4 + RAG2	No	No	No	No	No	*Cyclemmys, Testudo, Gopherus*
ND4 + RAG1 + RAG2	No	No	No	No	No	None
RAG1 + RAG2	No	No	No	No	No	None

Table 1b: Summary of the tree topologies recovered from maximum likelihood and Bayesian analyses, addressing the monophyly of Testudinidae, Bataguridae/Geoemydidae, Emydidae, the two emydid sub-clades, Emydinae, and Deirochelyinae, and noting if any of the genera represented by multiple species were recovered as monophyletic.

Analysis	Monophyly of Testudinidae	Monophyly of Bataguridae	Monophyly of Emydidae	Monophly of Emydinae	Monophyly of Deirochelyinae	Monophyly of genera with multiple species represented (each is noted)
Species level morphology + ND4 + RAG1 + AG2	Yes	No	No	No	No	*Terrapene* (including TMM 40688-93), Cuora (including *Pyxidea mouhotii*), Cyclemmys, Testudo, Geochelone (including *Dipsochelys dussemeiri*), *Gopherus*, *Rhinoclemmys, Emys*
Bayesian						
Specimen level morphology	Yes	No	No	No	No	None
Species level morphology	Yes	No	No	No	No	*Cyclemmys*
ND4 + RAG1	Yes	No	No	No	No	*Indotestudo, Gopherus, Geochelone*
ND4 + RAG2	No	No	No	No	No	*Emys*, *Gopherus, Geochelone* + *Dipsochelys*
ND4 + RAG1 + RAG2	No	No	No	No	No	*None*
RAG1 + RAG2	No	No	No	No	No	*Rhinoclemmys, Cyclemmys*
Species level morphology + ND4 + RAG1 + RAG2	No	No	No	No	No	*Terrapene* + TMM 40688-93, *Rhinoclemmys, Cyclemmys, Gopherus, Geochelone* + *Dipsochelys, Cuora* + *Pyxidea*

Figure 1: Dorsal view of holotype of TMM 40688-93.

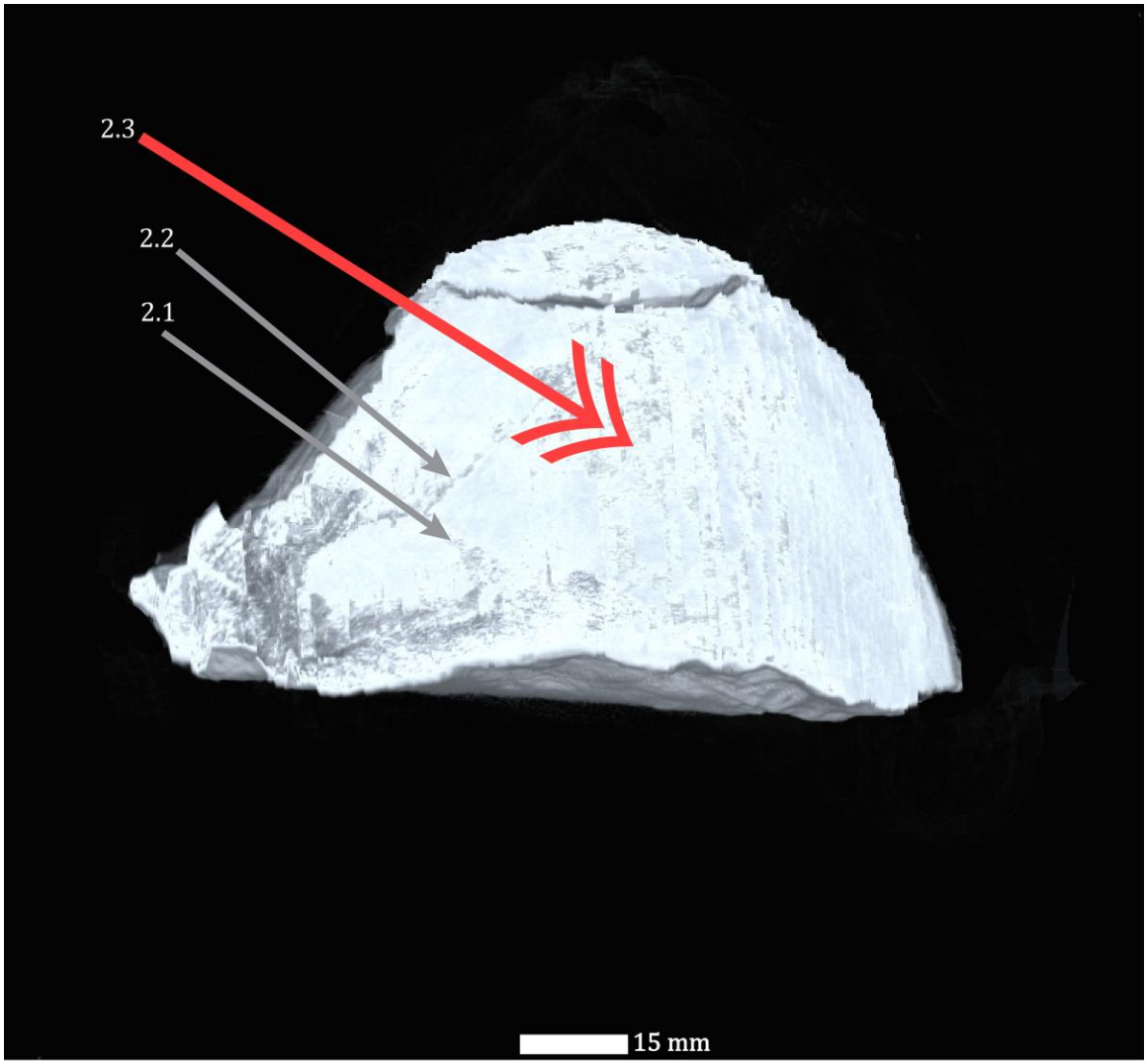

Figure 2: CT scan image of TMM 40688-93 from the anterior view. 2.1 and 2.2 indicate cracks along the surface, red arrow (2.3) indicates direction in which the crushed portion of the shell was pushed.

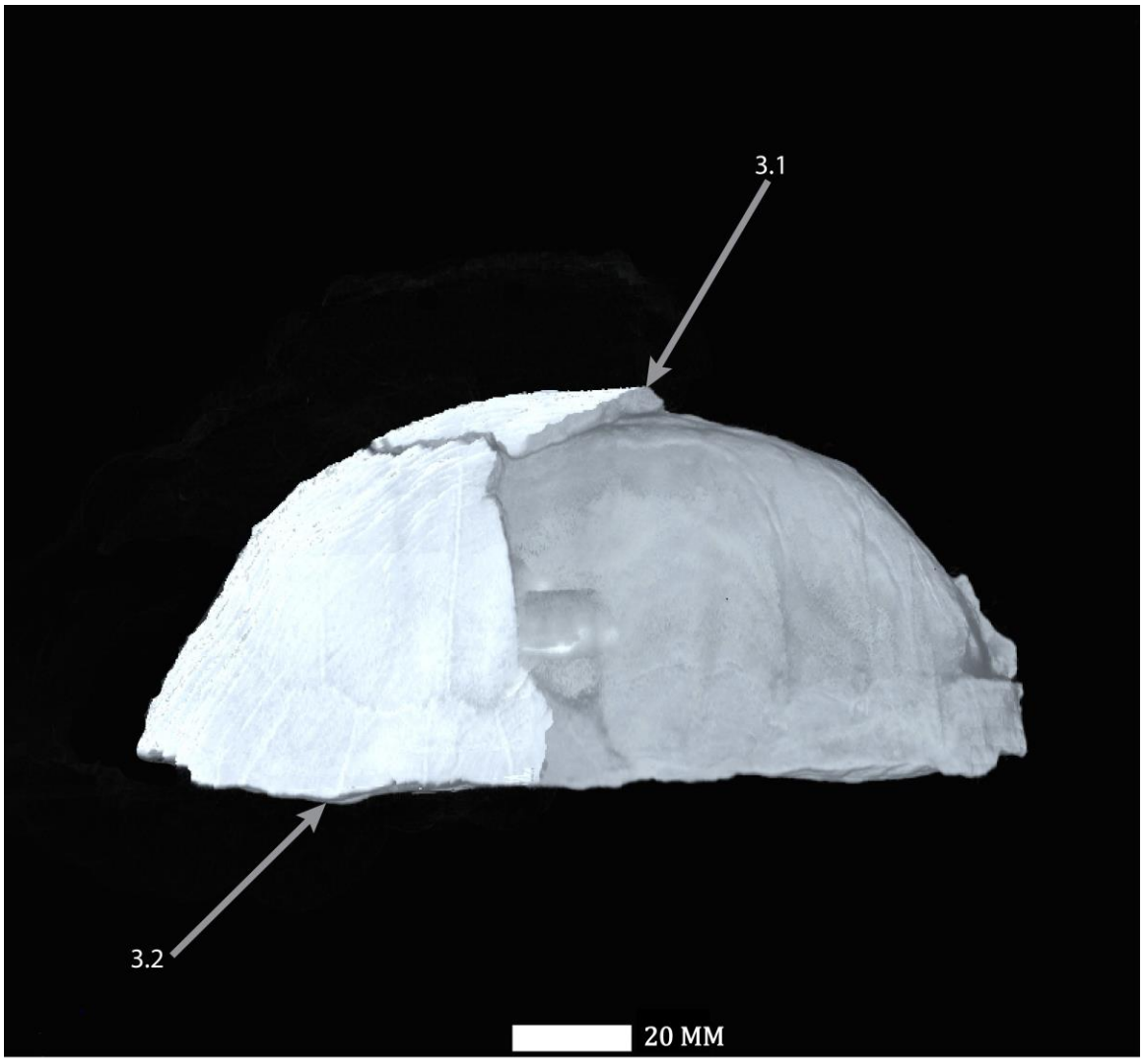

Figure 3: CT scan image of TMM 40688-93 from left lateral view, anterior is left. Arrow 3.1 indicates the highest point of the shell, just posterior to the midline of the carapace. Arrow 3.2 indicates the anterior peripherals.

Figure 4: Section of carapace of TMM 40688-93 showing three preserved neurals, anterior is left.

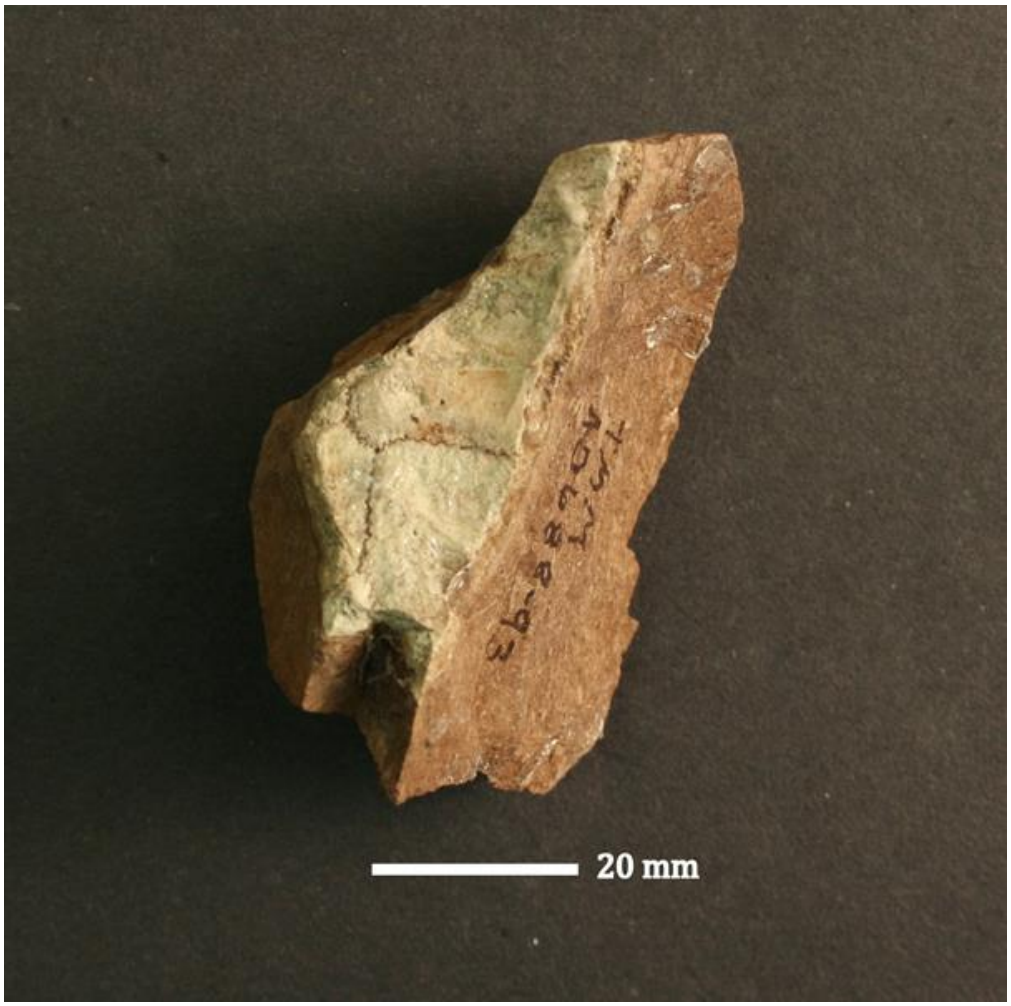

Figure 5: Section of carapace of TMM 40688-93 with portion of a neural and two costals preserved, anterior is left.

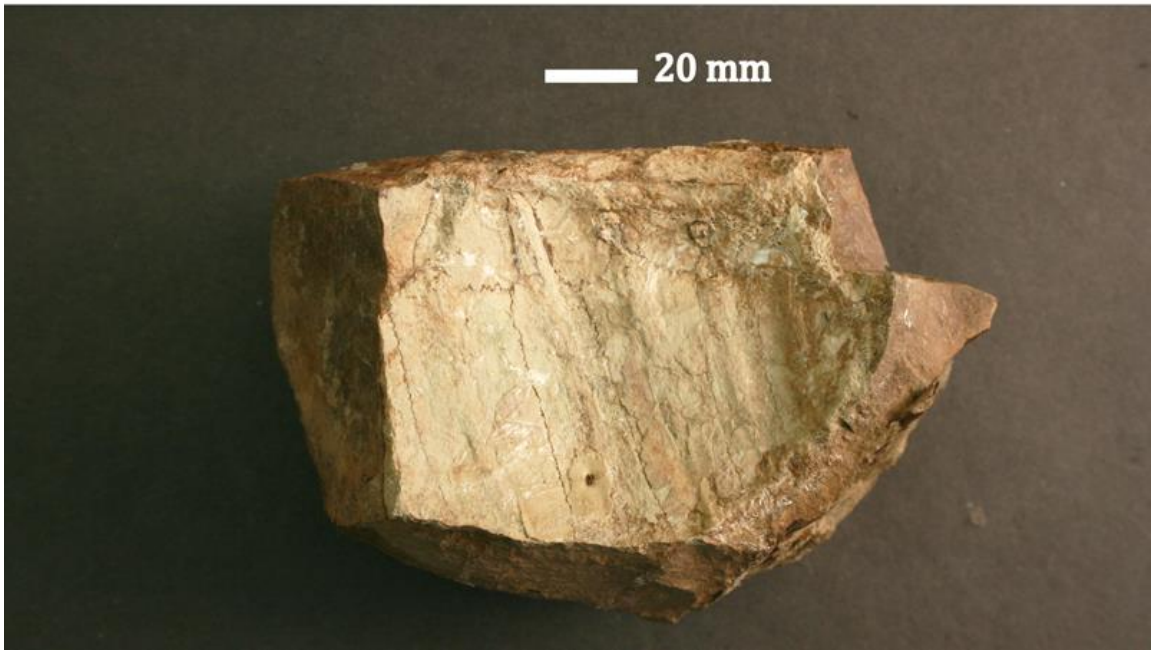

Figure 6: Section of carapace of TMM 40688-93 preserving five complete costals and portions of two more. Anterior is left; ventral is at the top.

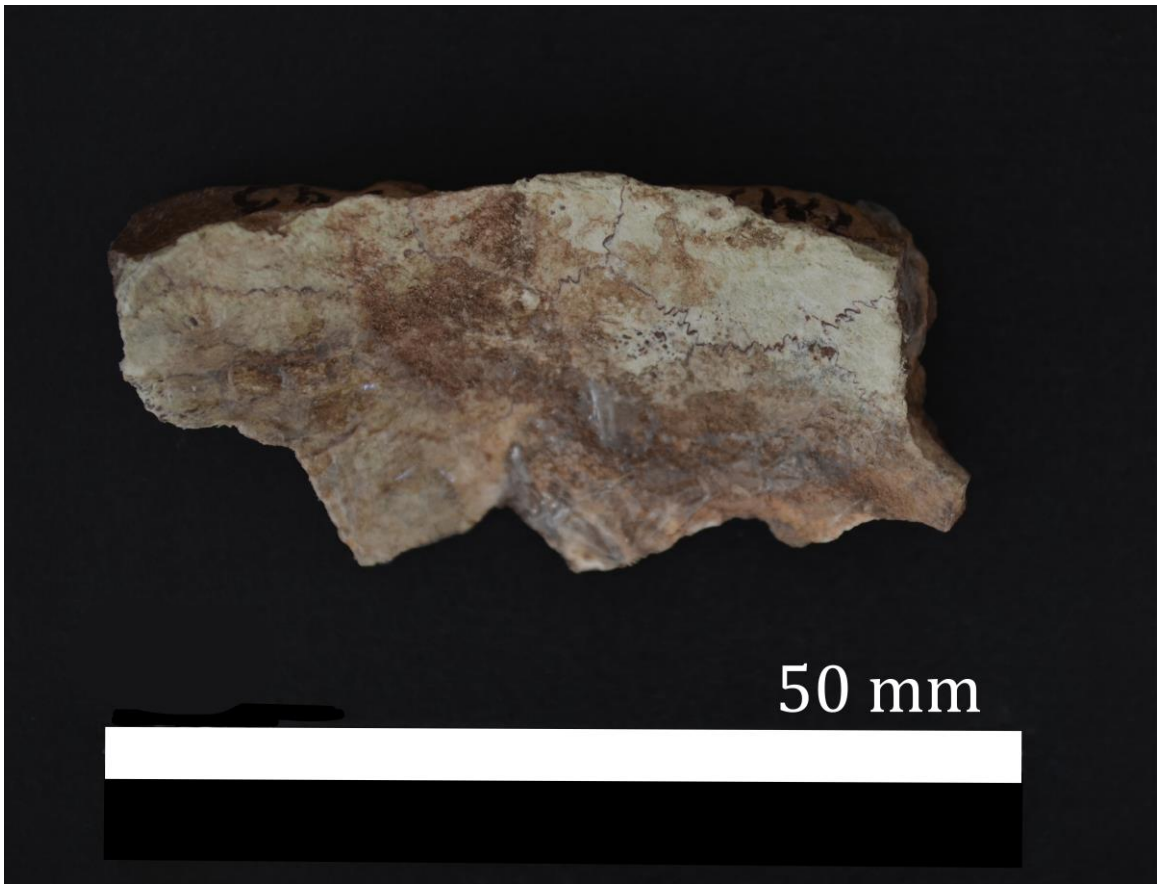

Figure 7: Section of carapace of TMM 40688-93 preserving a neural, portion of first suprapygal, and portion of eighth costal, anterior is left.

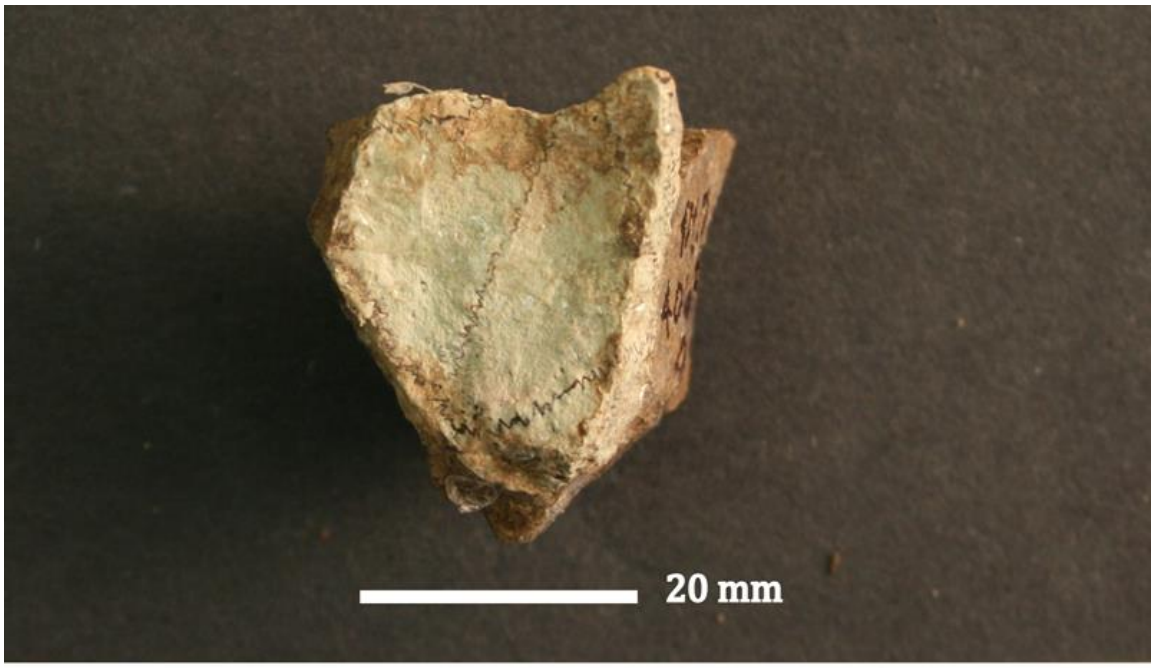

Figure 8: Section of carapace of TMM 40688-93 preserving both suprapygals, anterior and dorsal are left.

Figure 9: Section of carapace of TMM 40688-93 from preserving portion of three neurals and three costals, anterior is left.

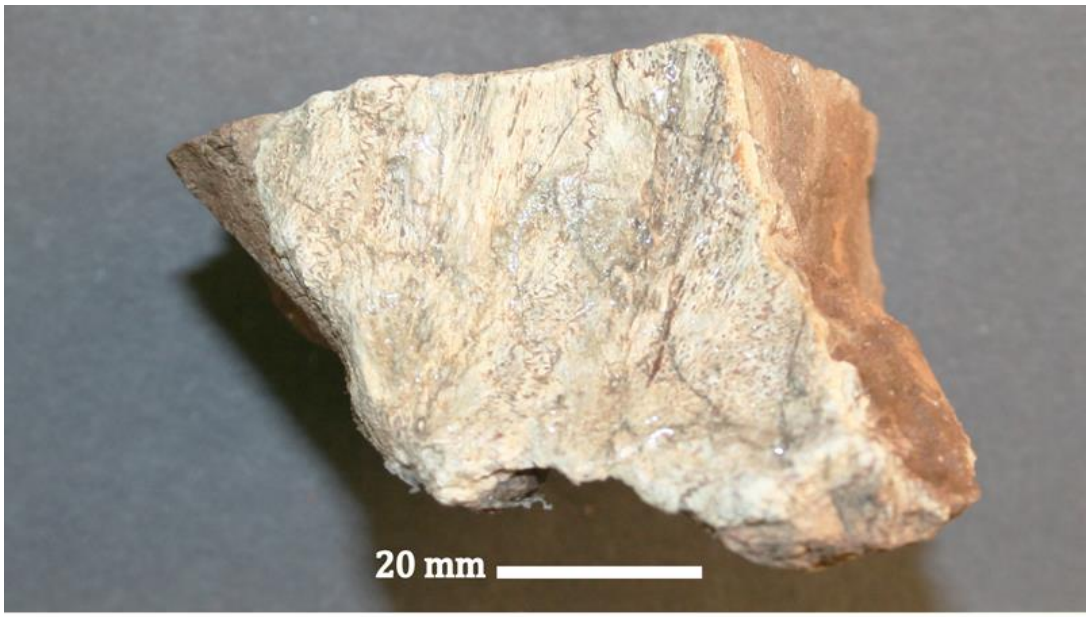

Figure 10: Section of carapace of TMM 40688-93 preserving portions of right costals and peripherals, anterior is to the left.

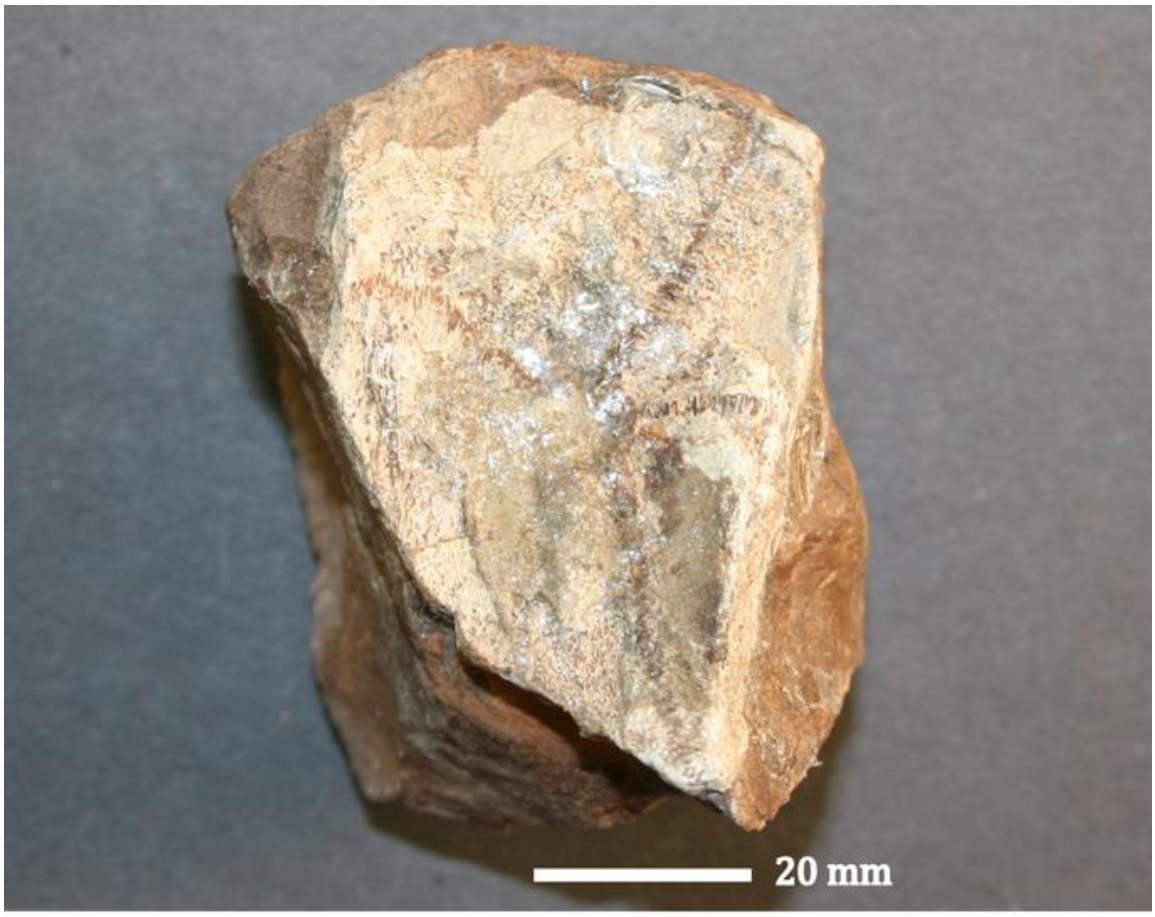

Figure 11: Section of carapace of TMM 40688-93 preserving portions of right costals, anterior is left.

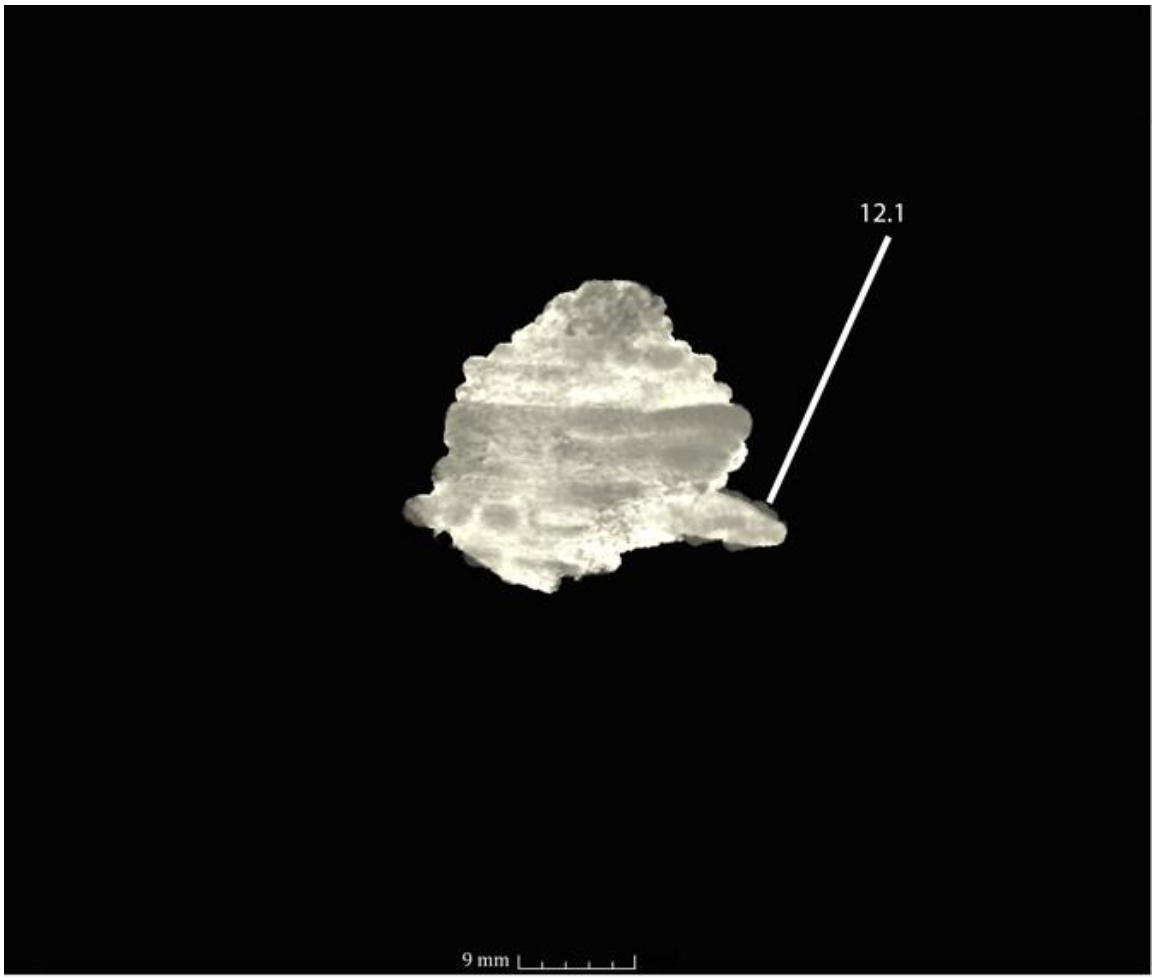

Figure 12: Dorsal view of nuchal of TMM 40688-93, 12.1 indicates the preserved costiform process.

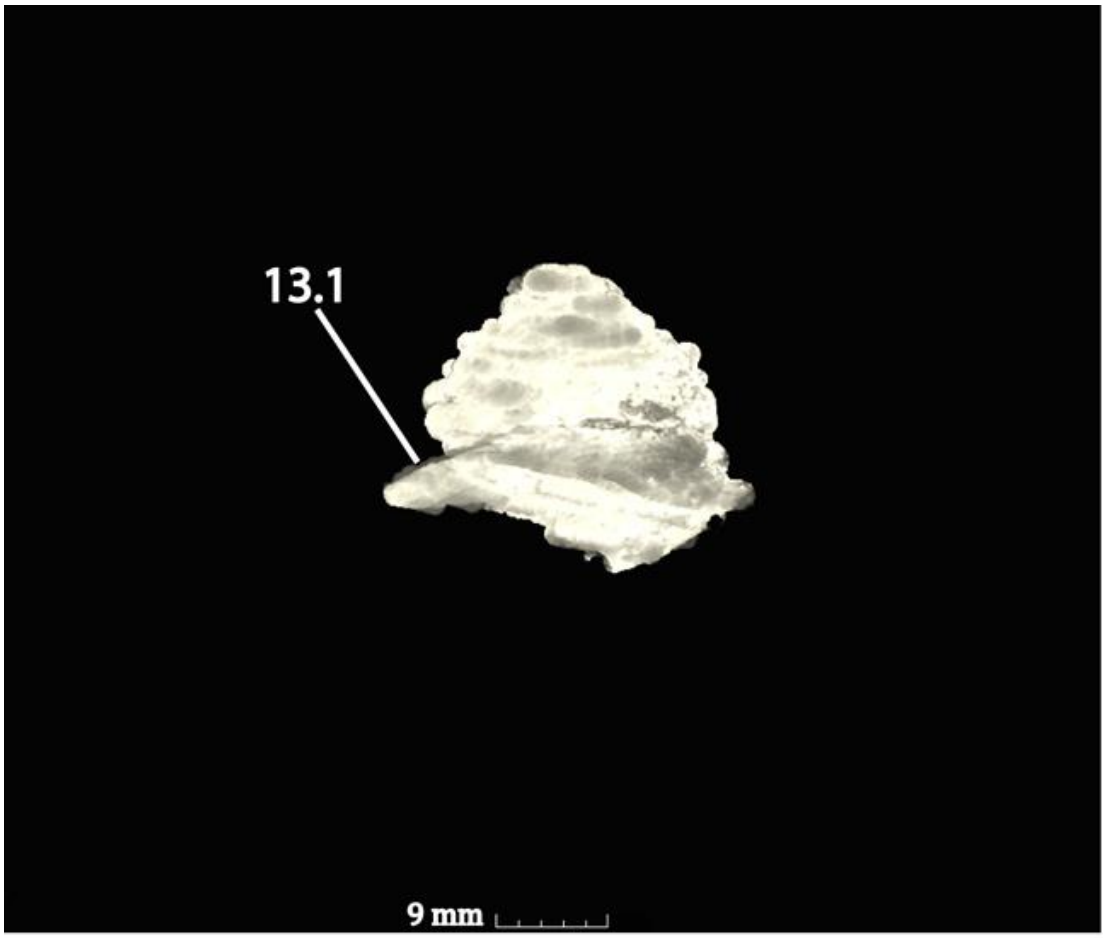

Figure 13: Ventral view of nuchal of TMM 40688-93, 13.1 indicates the costiform process.

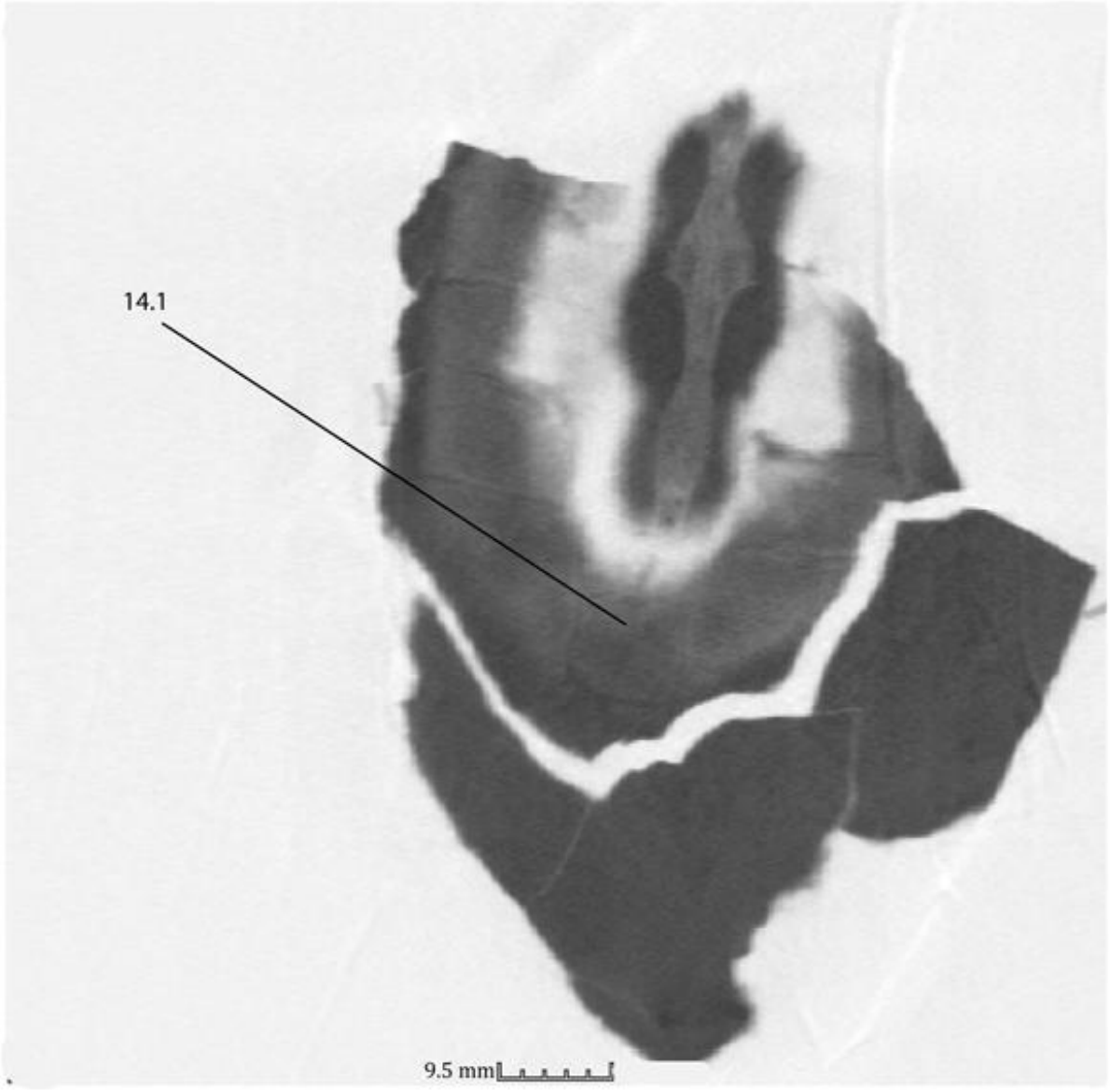

Figure 14: Dorsal view of CT slice of TMM 40688-93, 14.1 indicates the anterior portion first neural as seen in the CT slice, anterior is bottom.

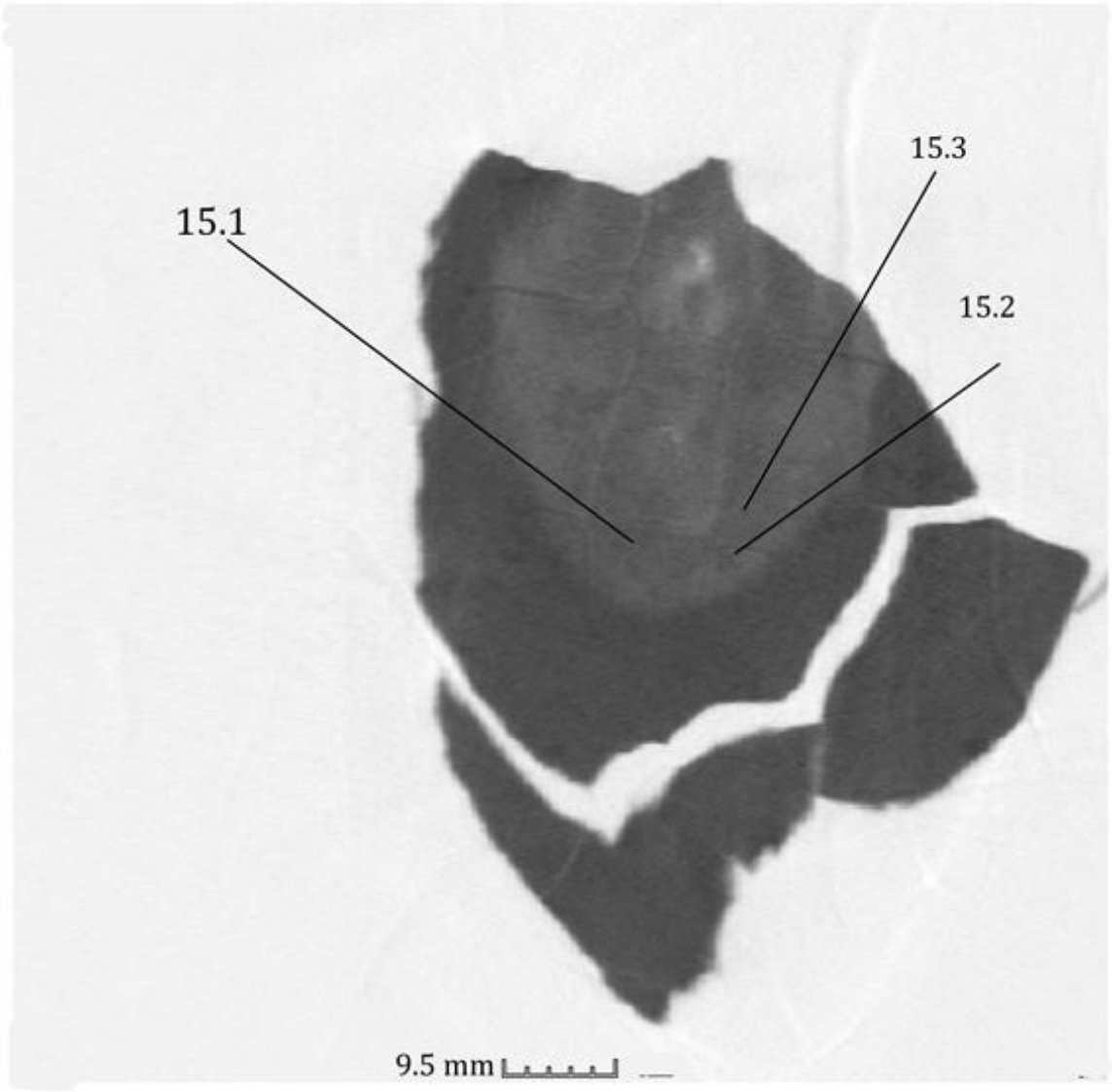

Figure 15: Dorsal view of CT slice of TMM 40688-93, 15.1 indicates the posterior portion of the first neural as seen in the CT slice, anterior is bottom. 15.2 and 15.3 indicate the first and second costal bones of the left side of the specimen.

Figure 16: Postero-dorsal view of TMM 40688-93 showing the neurals and portion of costals. Close-up inset shows neurals two, three, four, and five. Scale bar in close-up is also 20 mm.

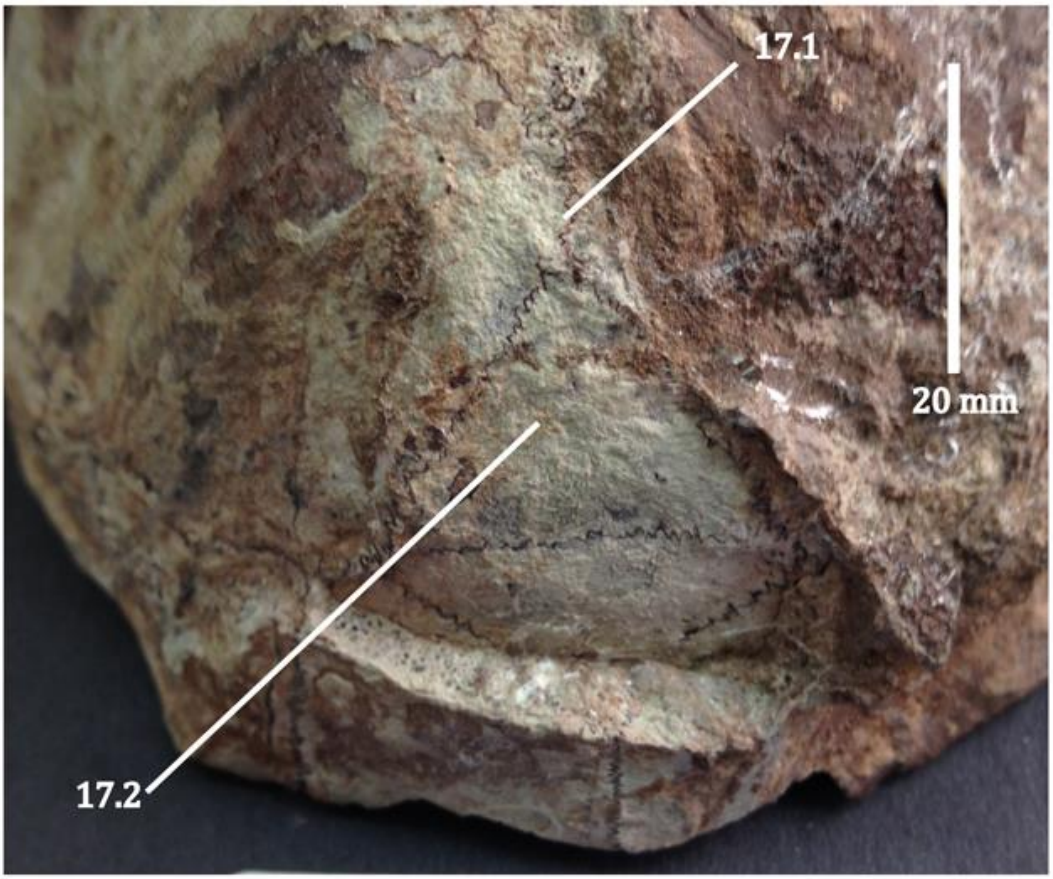

Figure 17: Posterio-dorsal view of TMM 40688-93. 17.1 shows the meeting at the mid-line of the eighth costals. 17.2 indicates the first suprapygal.

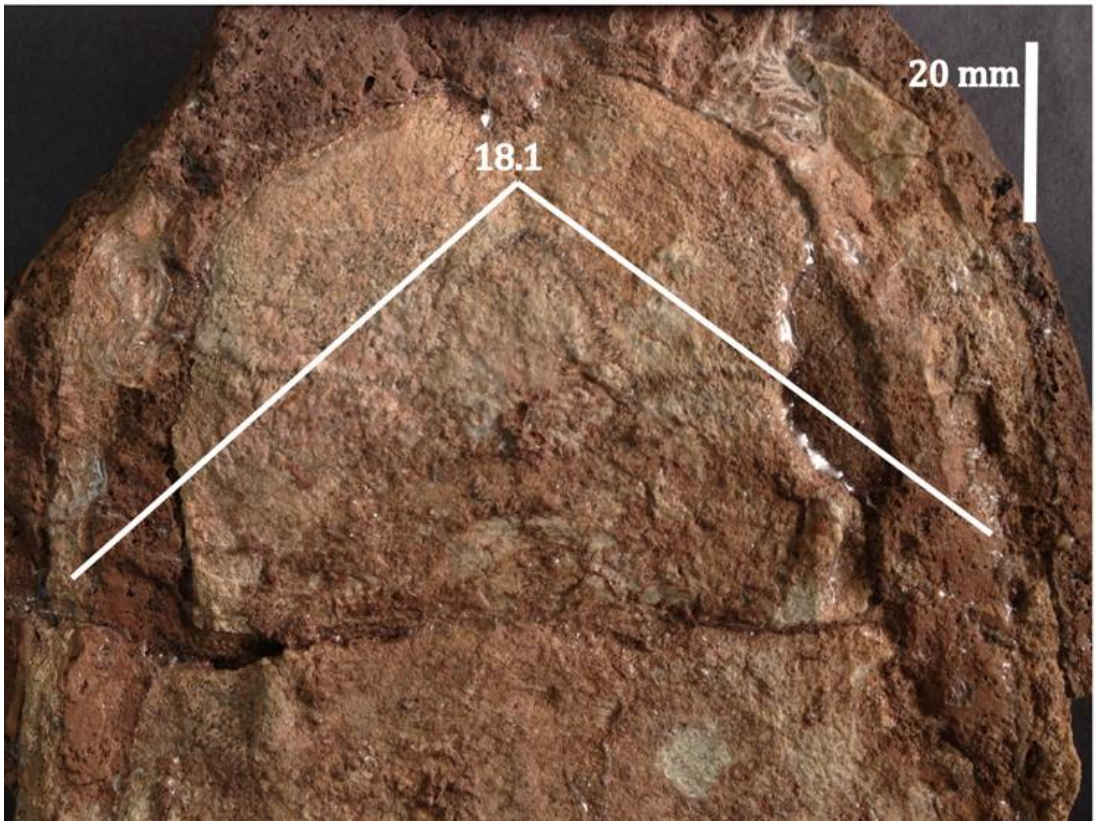

Figure 18: Ventral view of the plastron of TMM 40688-93. 18.1 indicates the lateral portions of the bridge peripherals that are preserved.

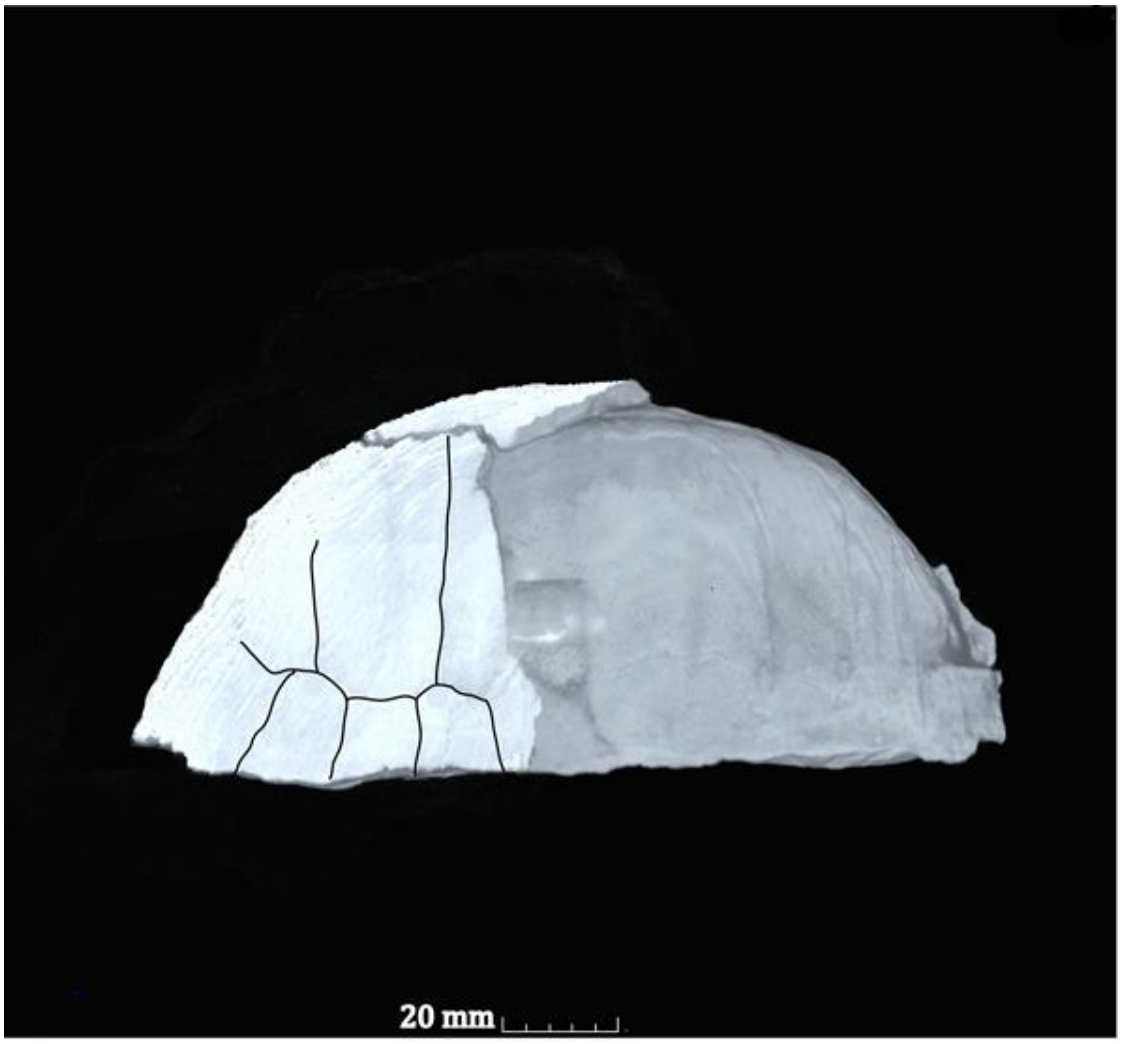

Figure 19: Left lateral view of CT image of TMM 40688-93, anterior is left. Black lines indicate boundaries of scutes as they appear in CT scan.

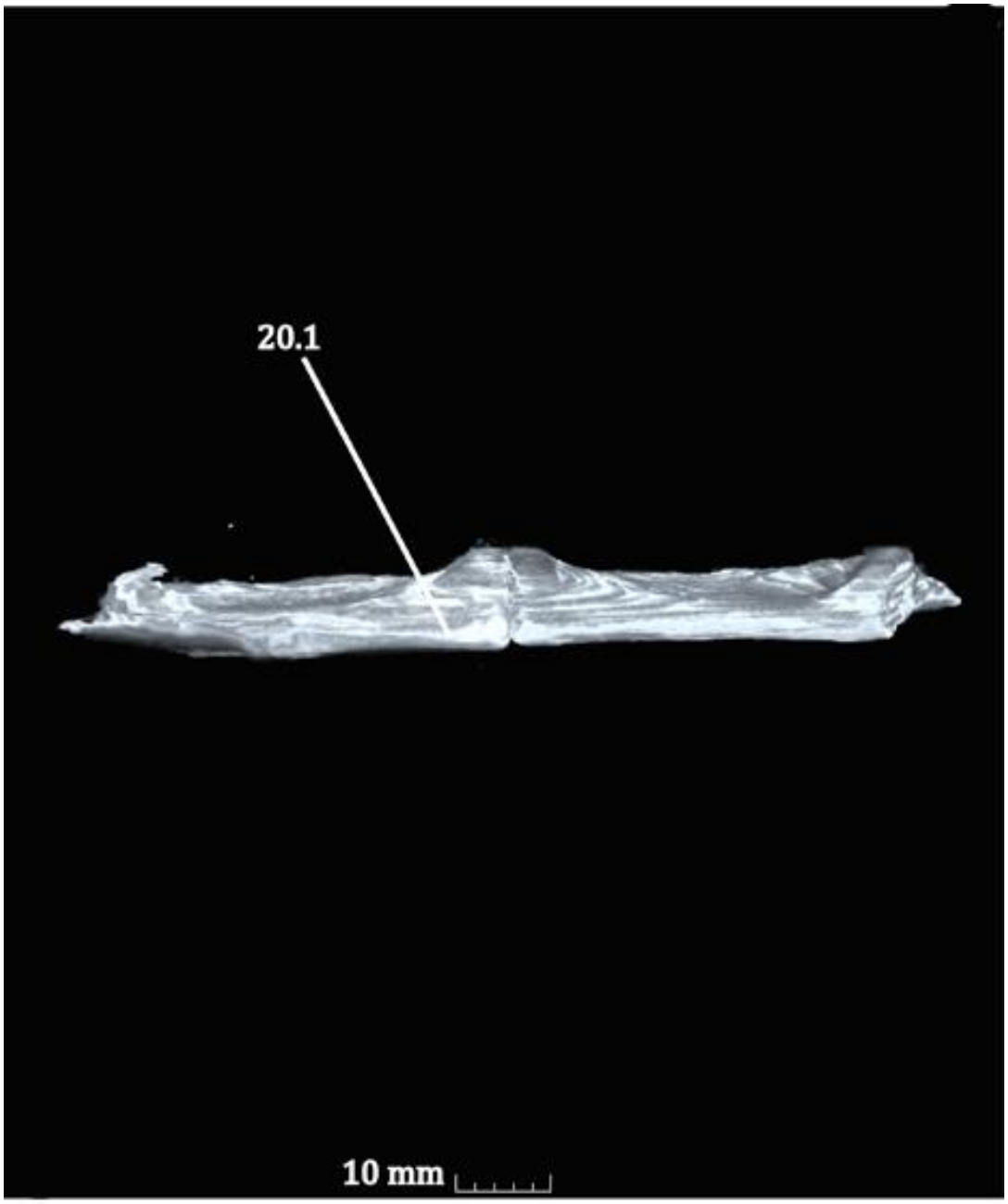

Figure 20: Anterior view of CT scan, of the posterior plastral lobe on TMM 40688-93. 20.1 indicates the groove that articulates with the anterior plastral lobe.

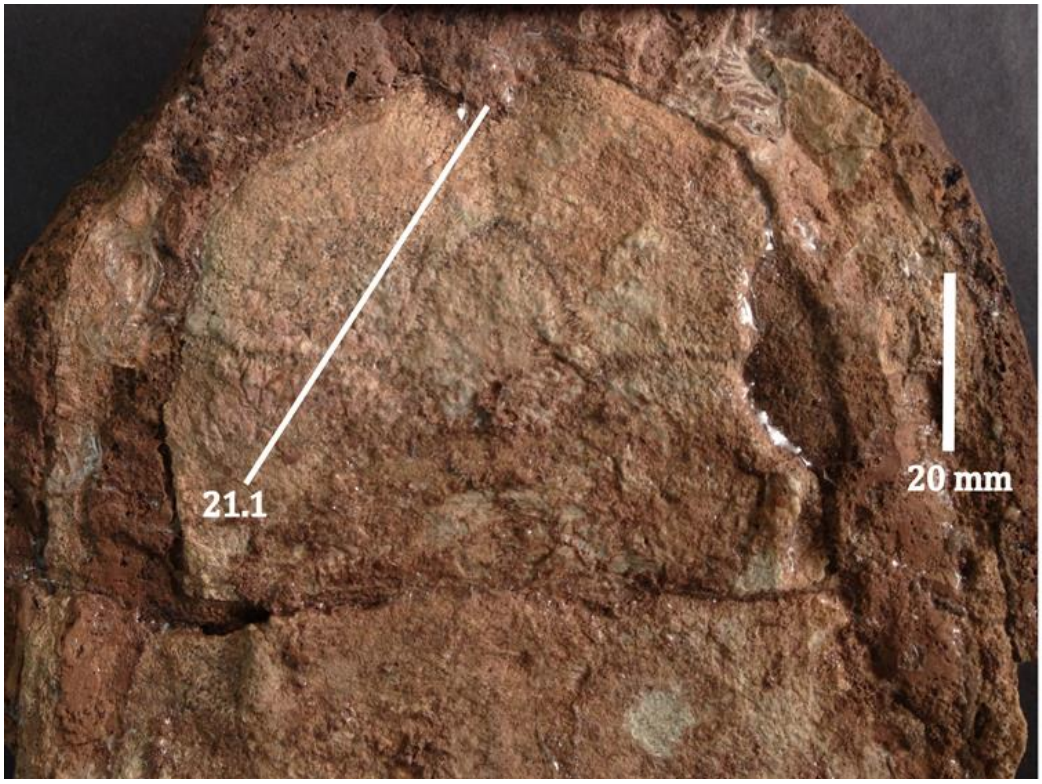

Figure 21: Ventral view of the plastron of TMM 40688-93. 21.1 indicates where the epiplastra are broken in preservation.

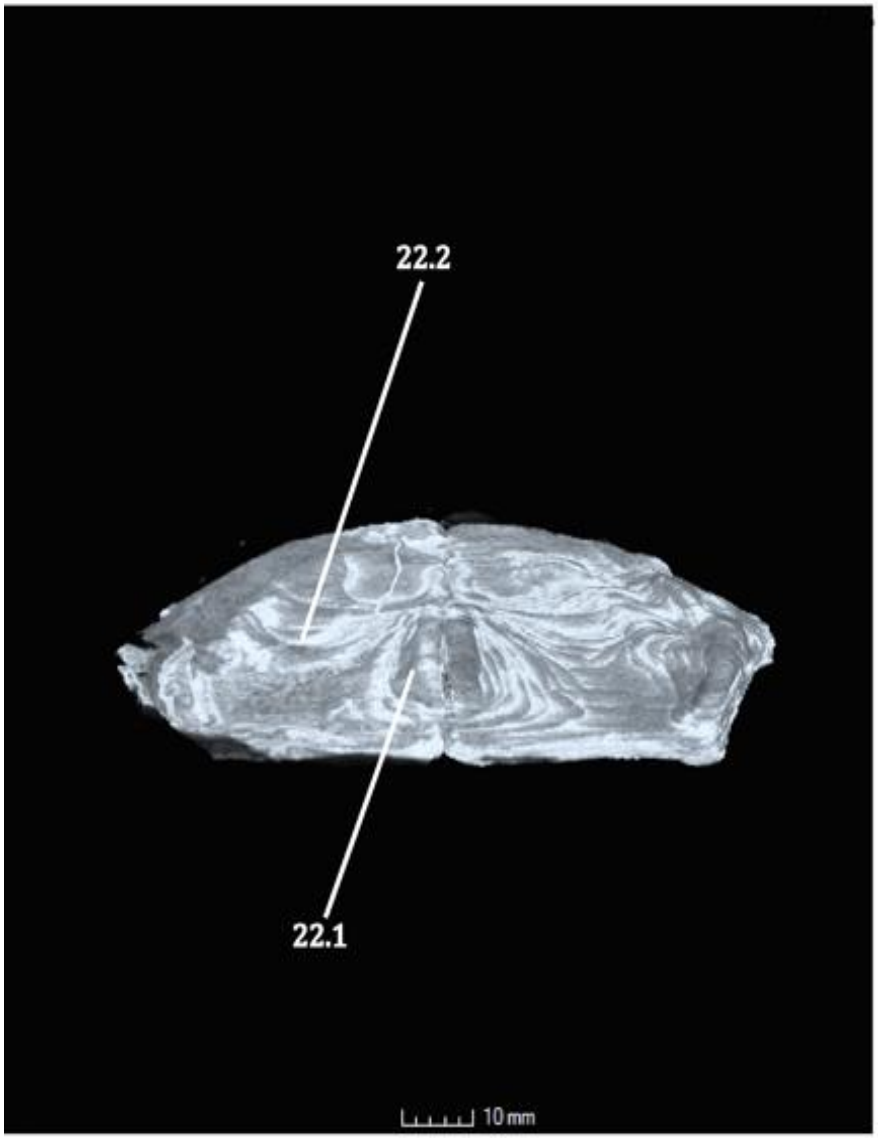

Figure 22: Antero-dorsal view of the CT scan of the posterior plastral lobe of TMM 40688-93. 22.1 indicates the medial ridge of the dorsal surface. 22.2 indicates the two concavities found lateral to the medial ridge.

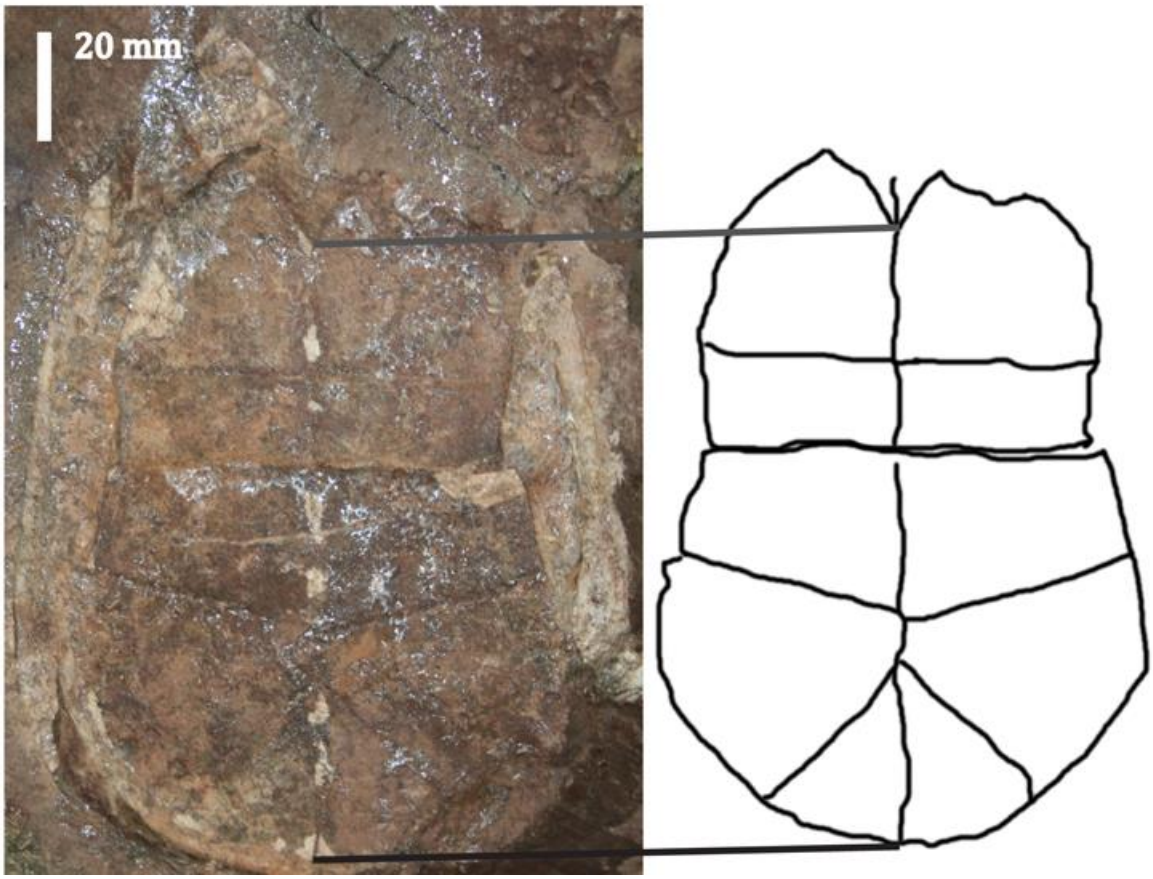

Figure 23: Impression of the scutes of TMM 40688-93, preserving the ventral view and line drawing interpretation of the sections of scutes that are preserved.

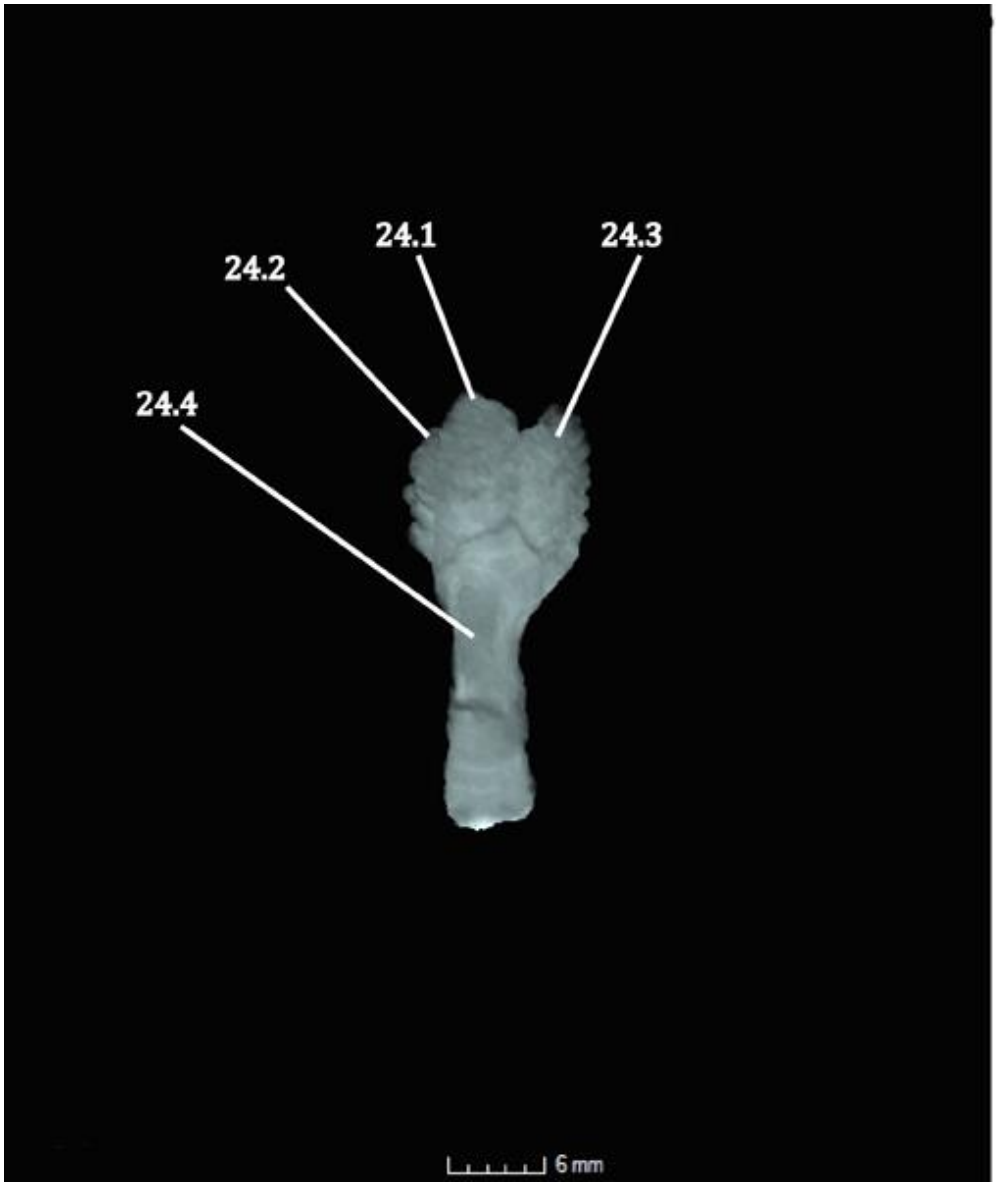

Figure 24: Cranial view of CT scan showing the left humerus of TMM 40688-93. 24.1 is the head, 24.2 cranial tuberculum, 24.3 caudal tuberculum, 24.4 corpus.

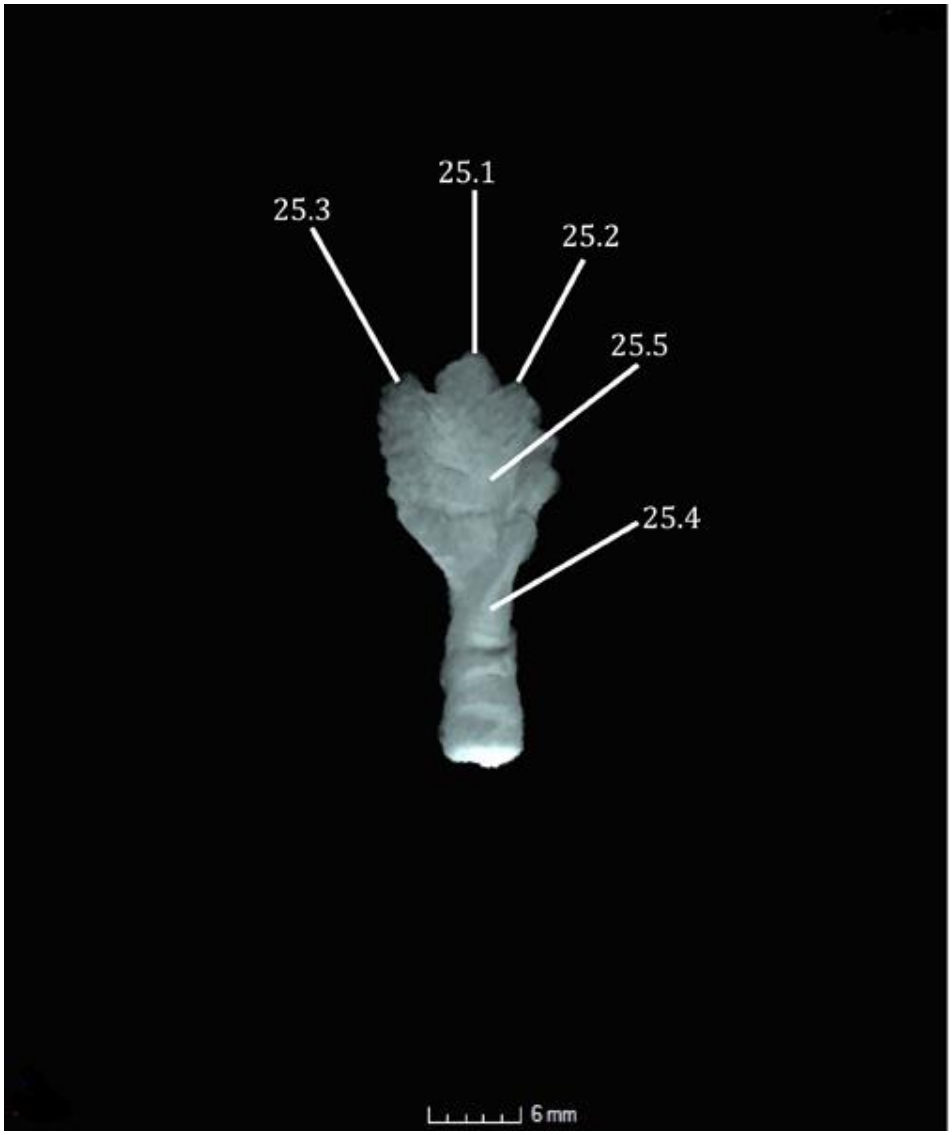

Figure 25: Caudal view of CT scan of left humerus of TMM 40688-93. 25.1 head of humerus, 25.2 cranial tuberculum, 25.3 caudal tuberculum, 25.4 corpus, 25.5 intertubercularis fossa.

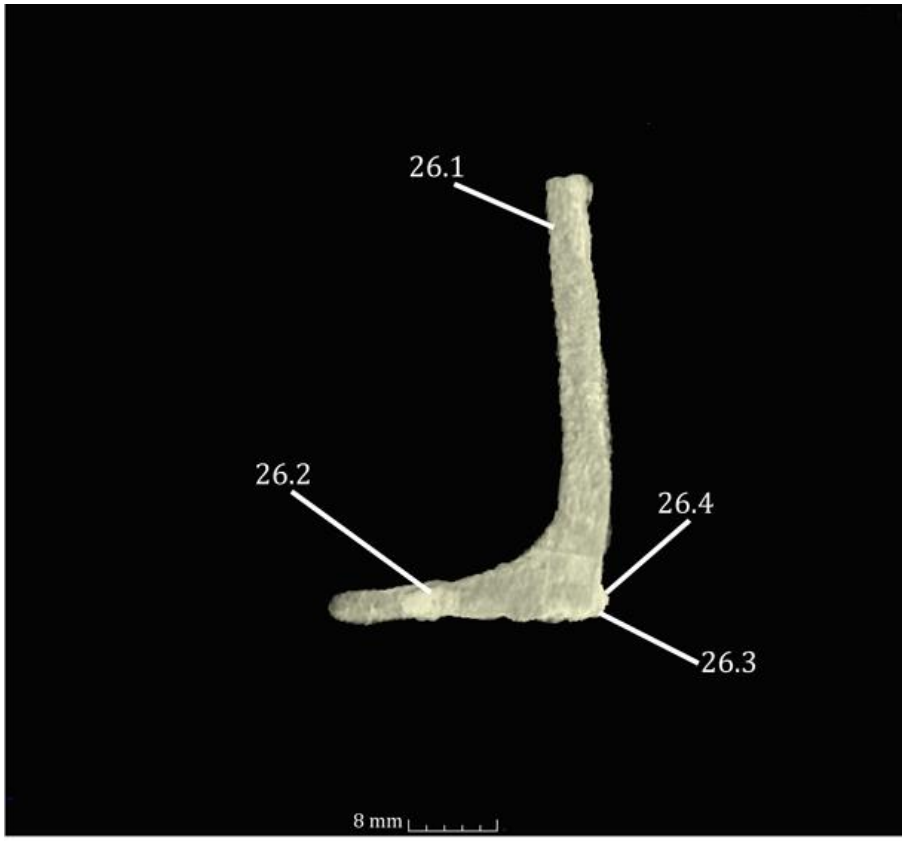

Figure 26: CT scan of the scapula of TMM 40688-93. 26.1 scapular process, 26.2 acromial process, 26.3 glenoid fossa, 26.4 attachment flange for triceps brachii.

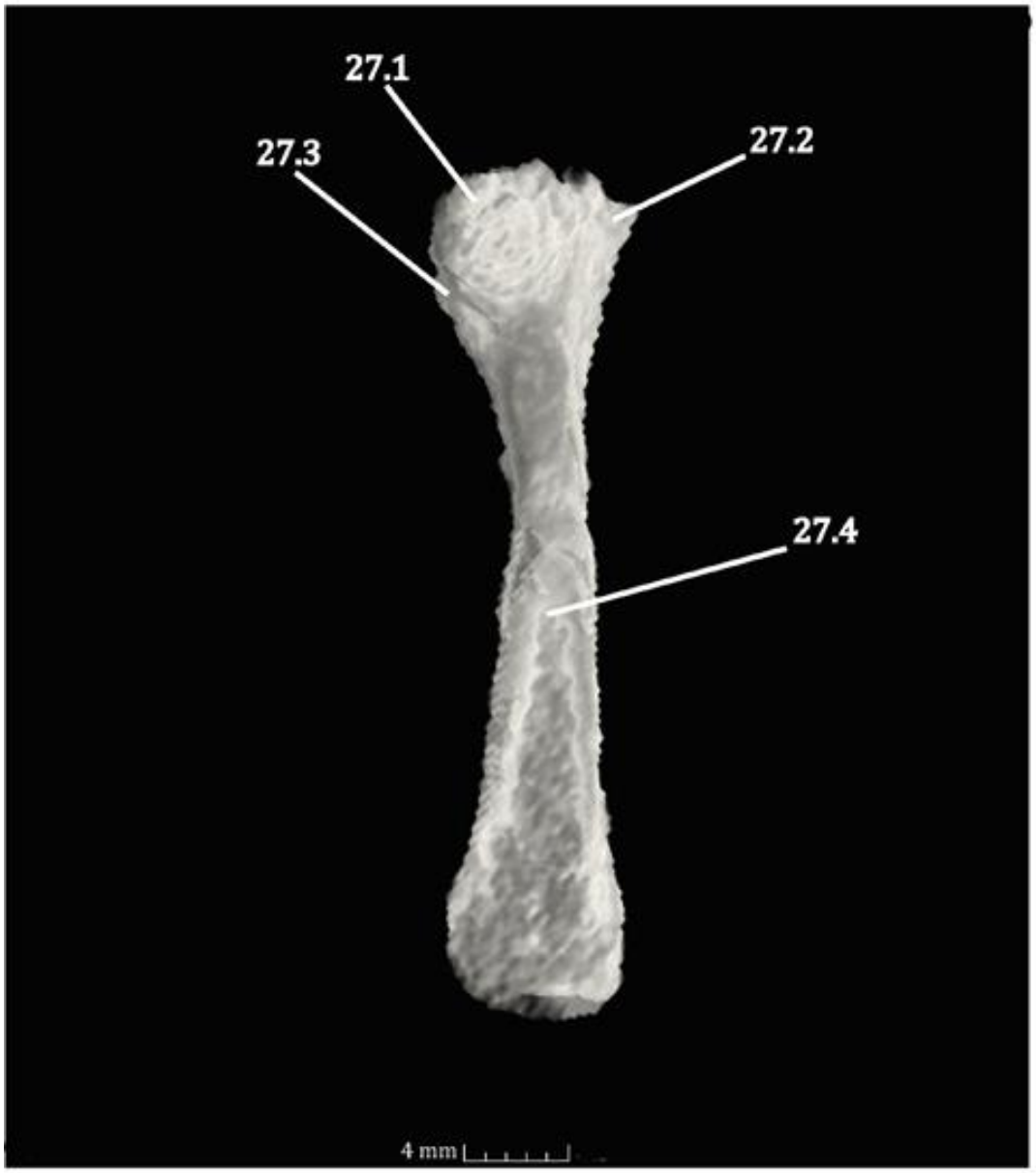

Figure 27: Cranial view of the left femur of TMM 40688-93. 27.1 head of the femur, 27.2 major trochanter, 27.3 minor trochanter, 27.4 corpus.

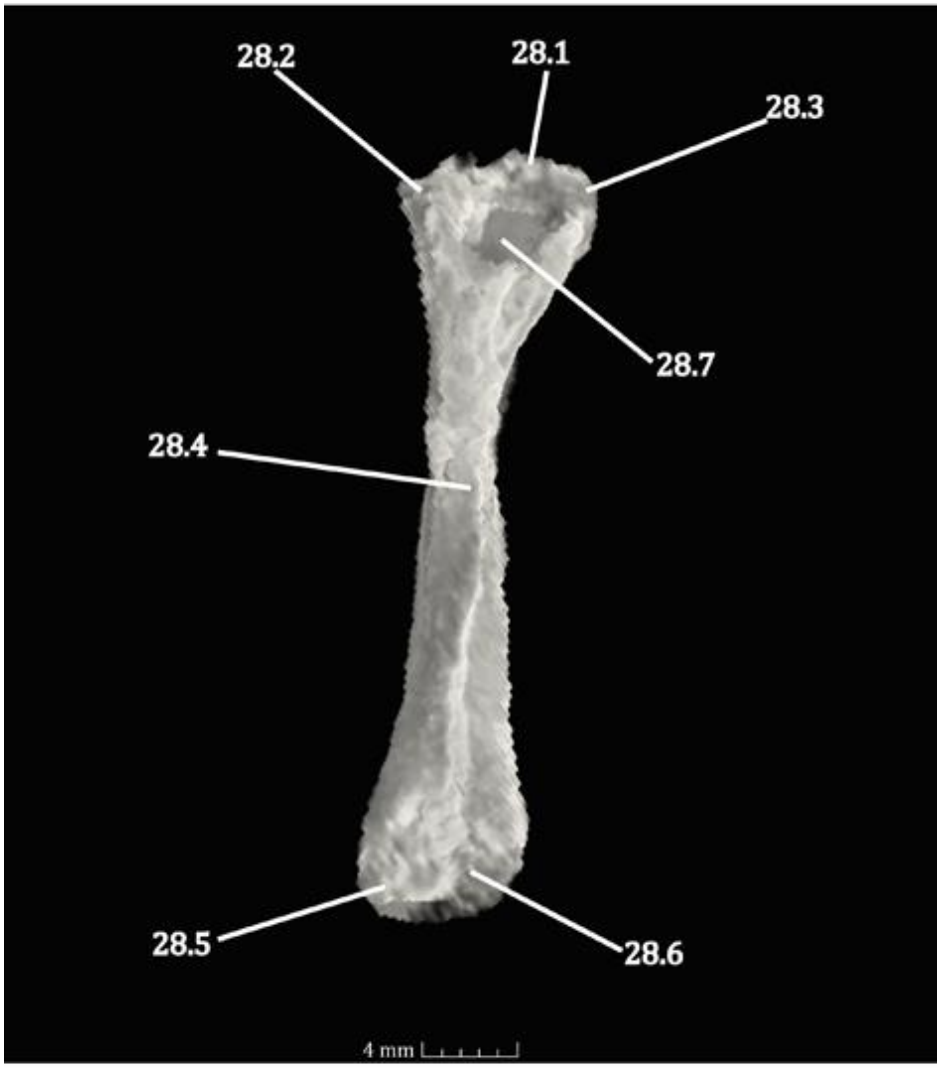

Figure 28: Caudal view of CT scan of the left femur of TMM 40688-93. 28.1 head, 28.2 major trochanter, 28.3 minor trochanter, 28.4 corpus, 28.5 tibial condyle, 28.6 fibular condyle, 28.7 trochanteric fossa.

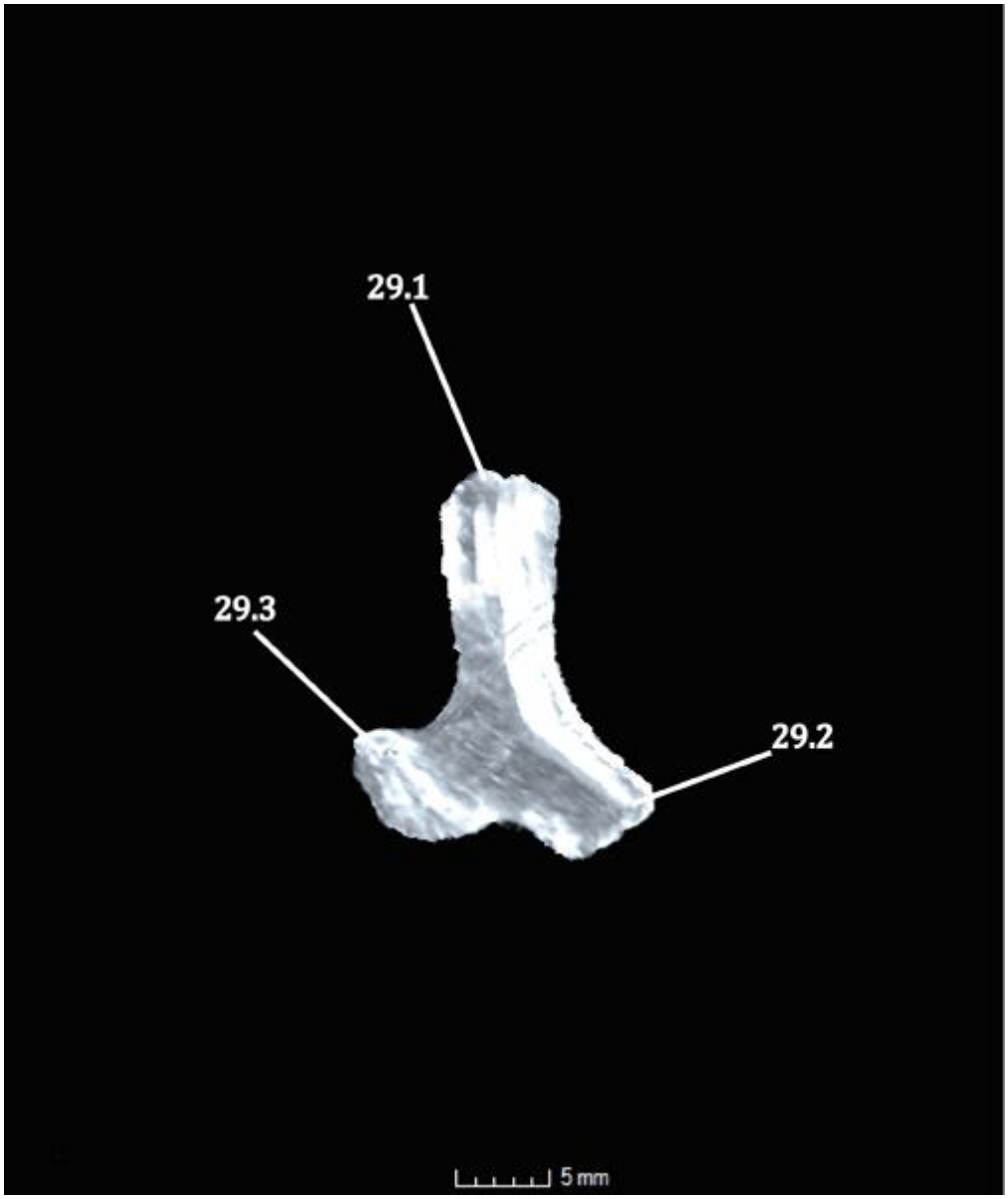

Figure 29: Dorsal view of CT scan of the left ischium of TMM 40688-93. 29.1 ischial-pubic tuberculum, 29.2 acetabular process, 29.3 lateral process of the ischium.

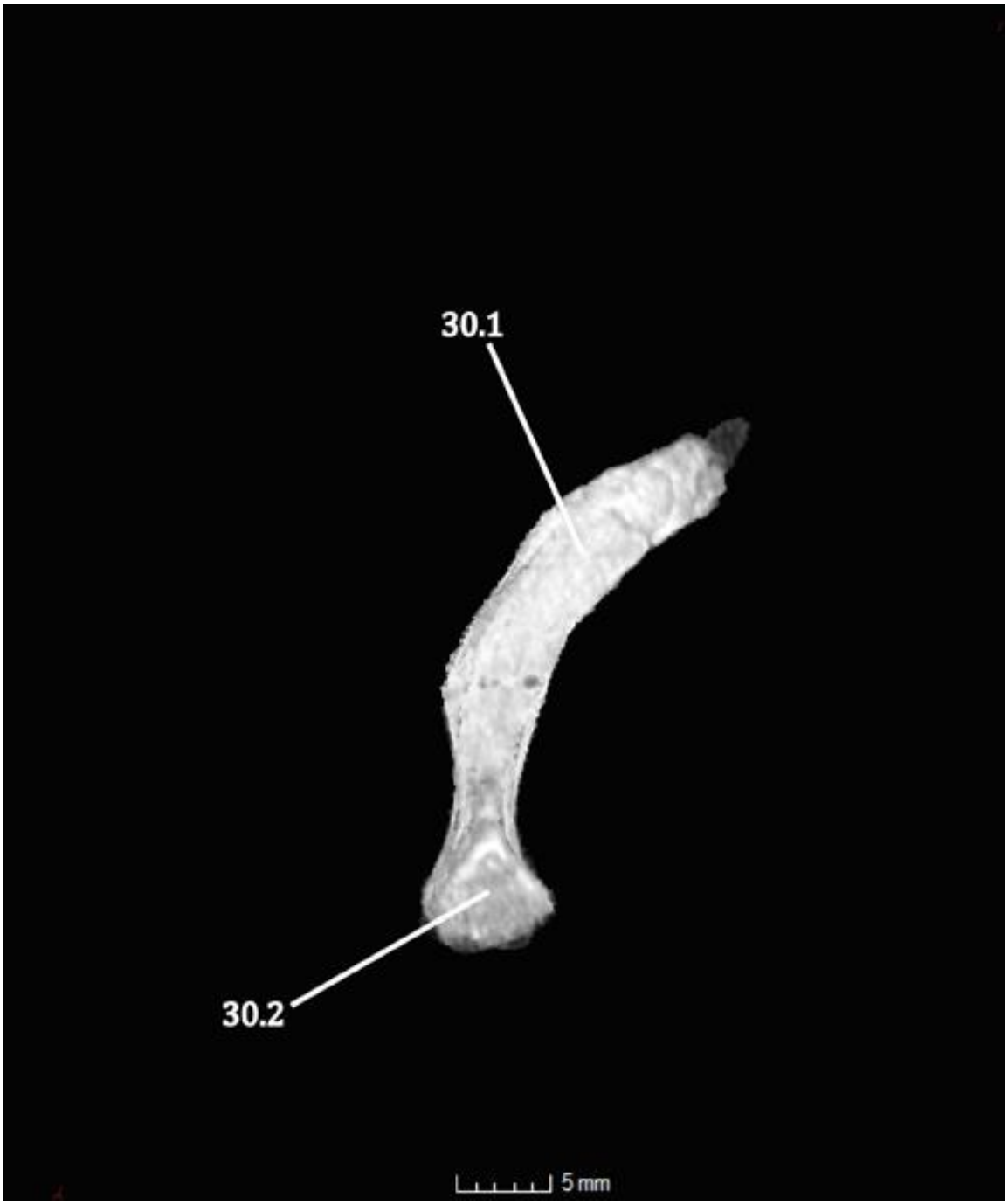

Figure 30: Lateral view of CT scan of the left illium of TMM 40688-93. 30.1 body of the illium, 30.2 acetabulum.

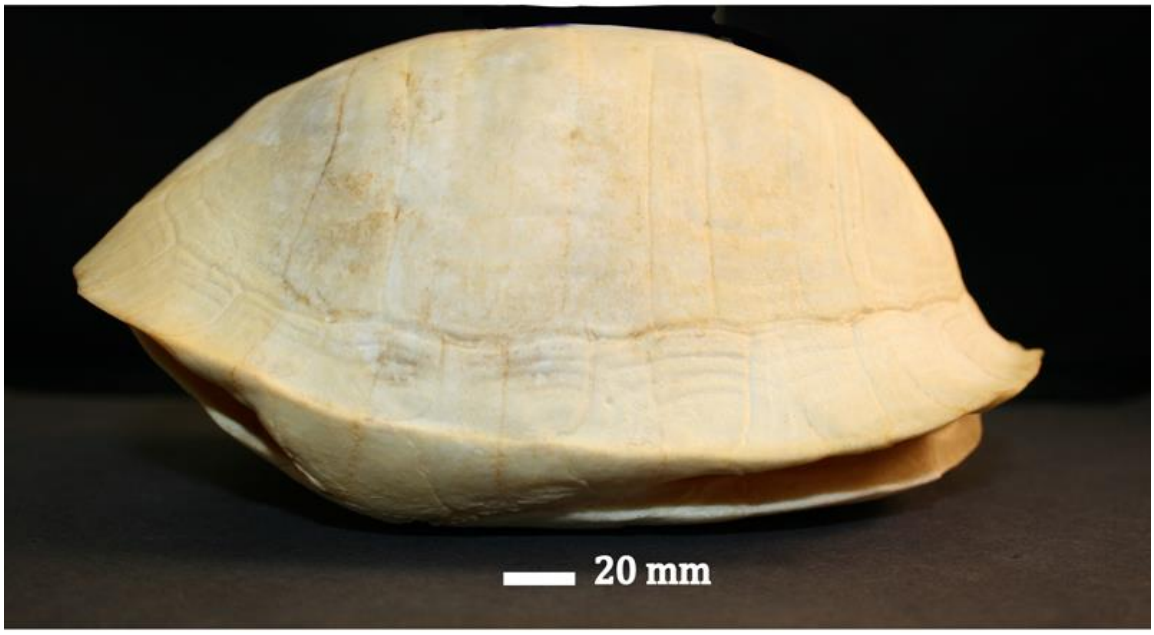

Figure 31: Left lateral view of *Terrapene carolina major* CAS 228375, anterior is left.

Figure 32: Left lateral view of *Cuora amboinensis* CAS 228419, anterior is left.

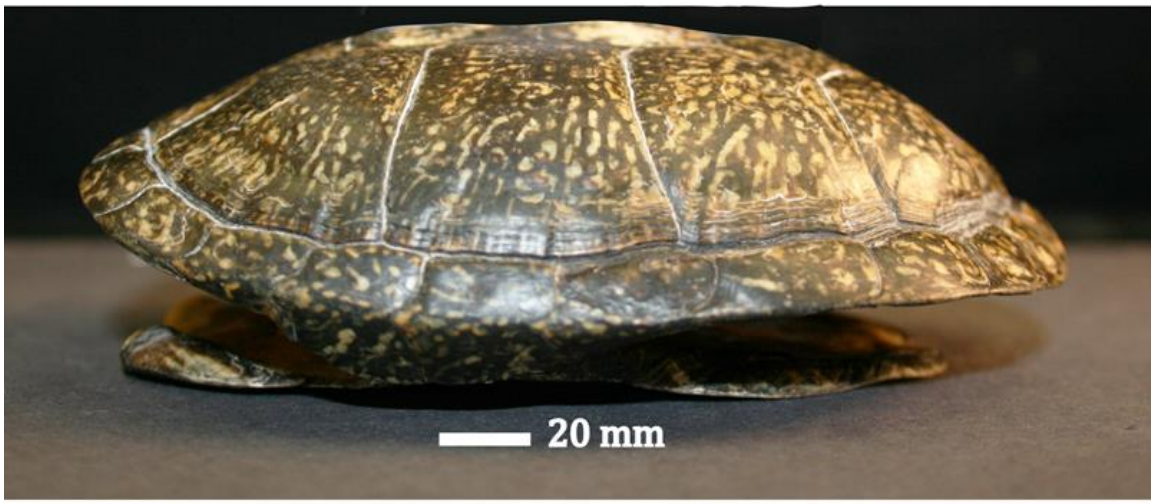

Figure 33: Left lateral view of *Emys orbicularis* CAS 228347, anterior is left.

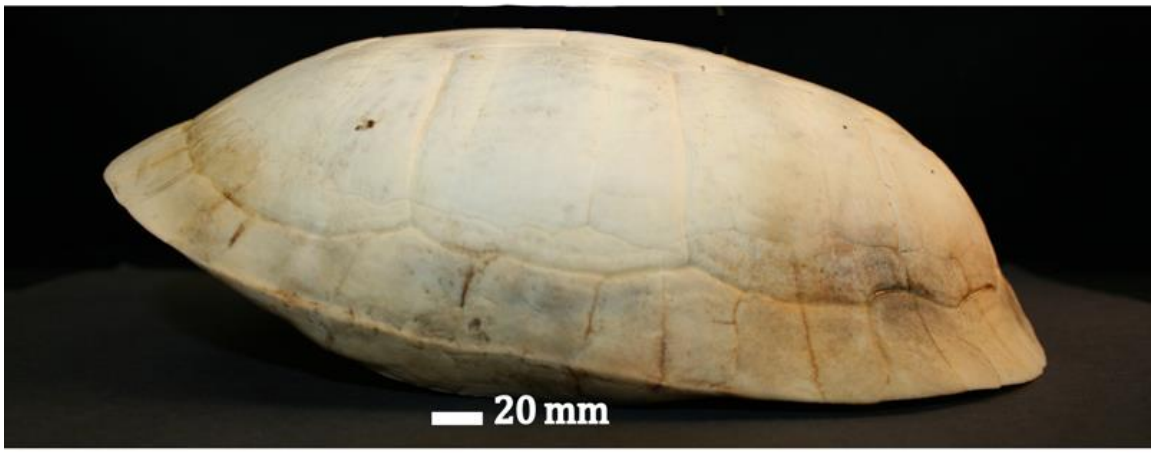

Figure 34: Left lateral view of *Emydoidea blandingii* CAS 228373, anterior is left.

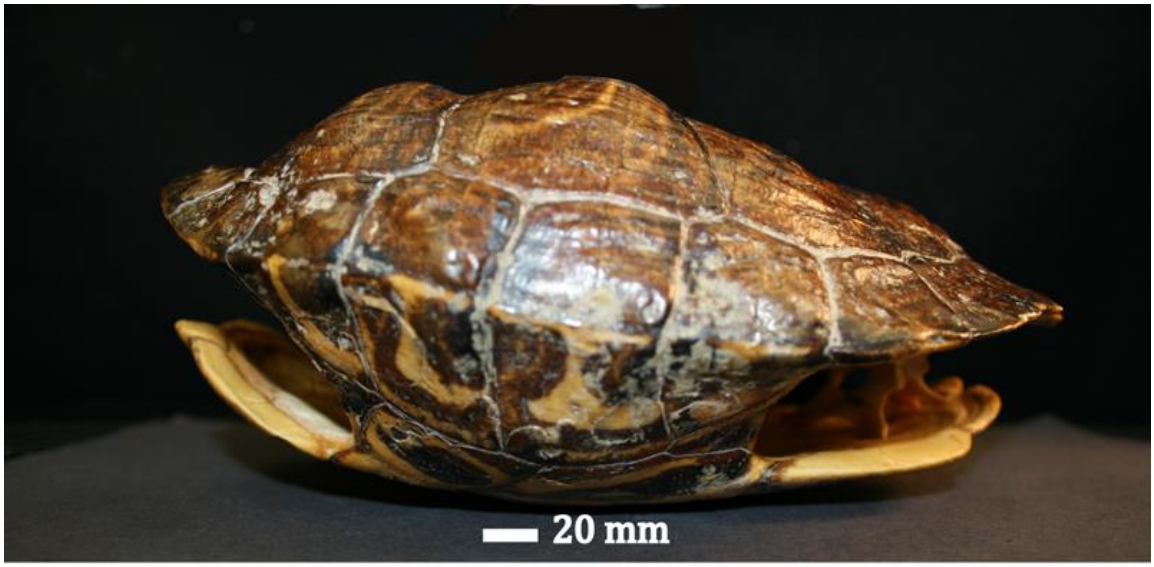

Figure 35: Left lateral view of *Trachemys scripta* TMM M-12134, anterior is left.

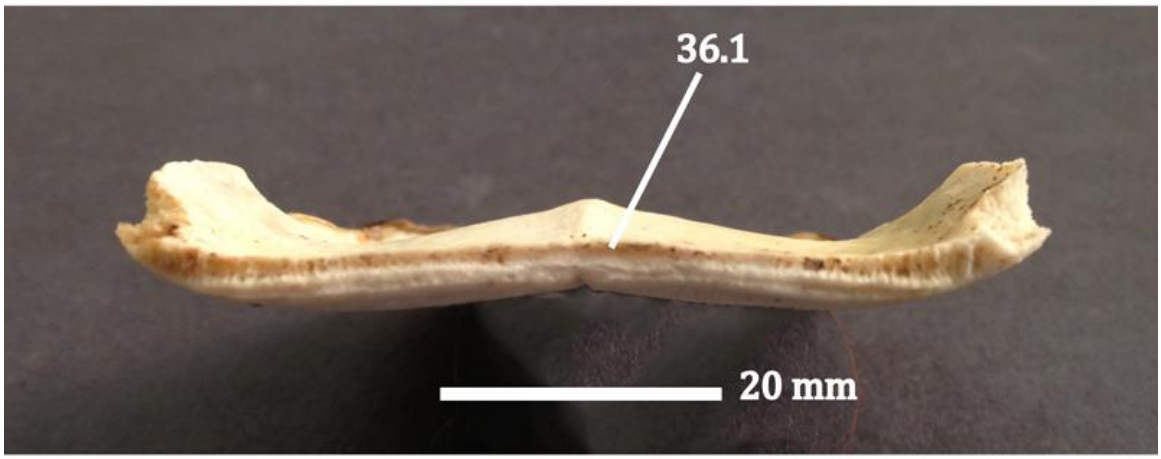

Figure 36: Anterior-dorsal view of posterior plastral lobe of *Terrapene coahuila* TNHC 69803. 36.1 indicates the groove that forms the articulation surface for the anterior plastral lobe along the plastral hinge.

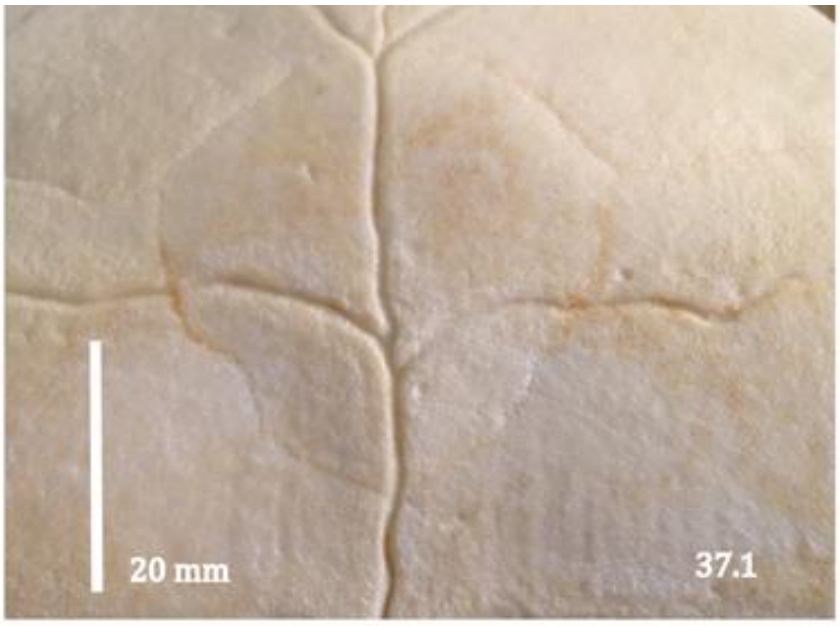

Figure 37: Ventral views of entoplastra from *Terrapene carolina major* CAS 228375 (37.1), and *Cuora amboinensis* CAS 228412 (37.2).

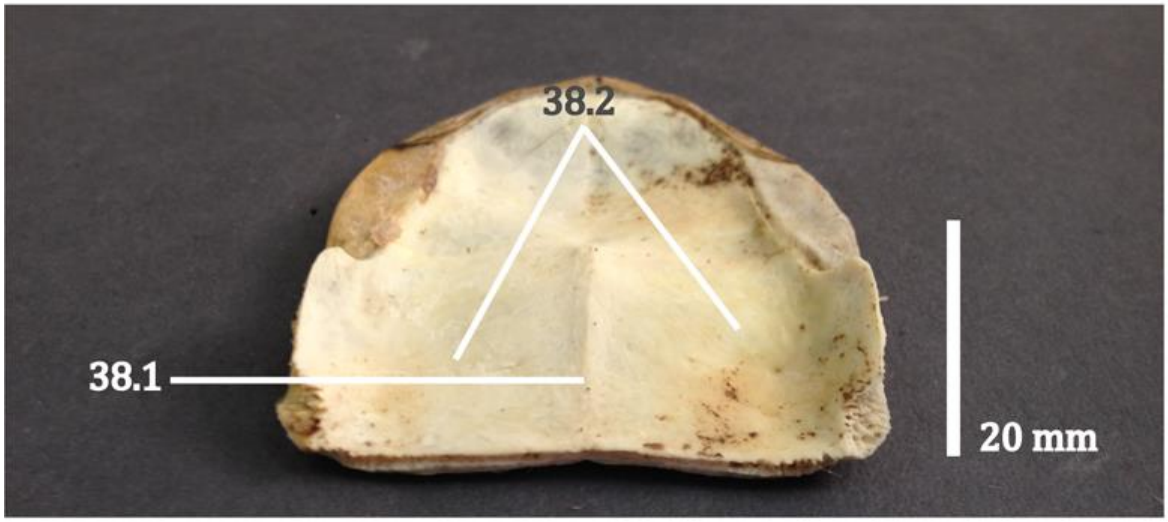

Figure 38: Anterio-dorsal view of the posterior lobe of *Terrapene coahuila* TNHC 69803. 38.1 indicates the medial ridge present in *T. coahuila*. 38.2 indicates the two concavities lateral to the medial ridge.

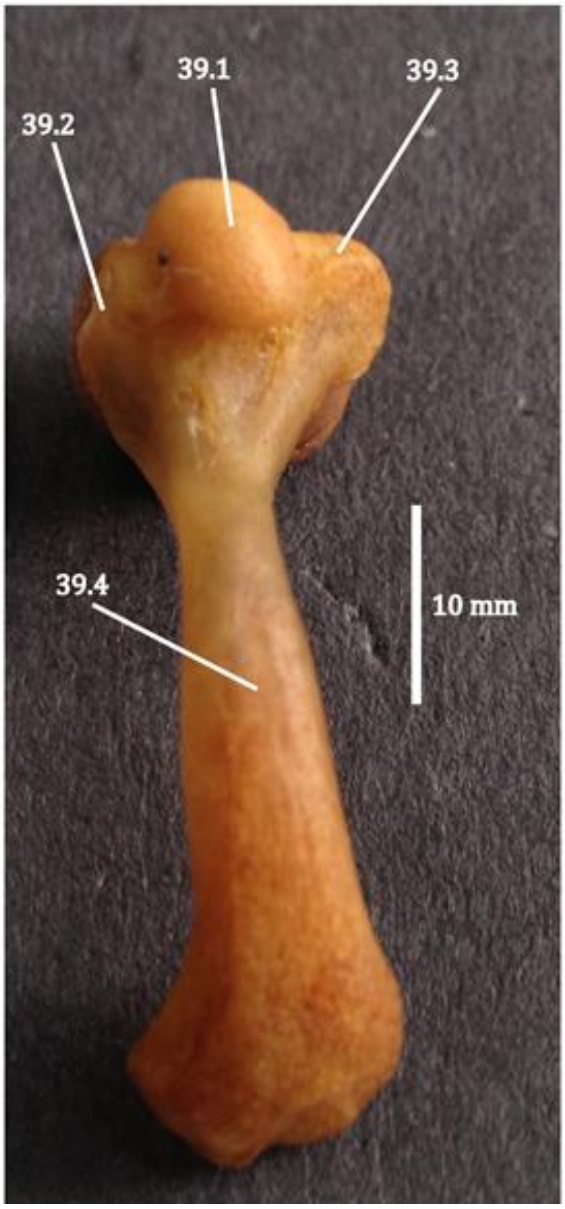

Figure 39: Cranial view of left humerus of *Emys orbicularis* CAS 228347. 39.1 head of the humerus, 39.2 cranial tuberculum, 39.3 caudal tuberculum, 39.4 corpus.

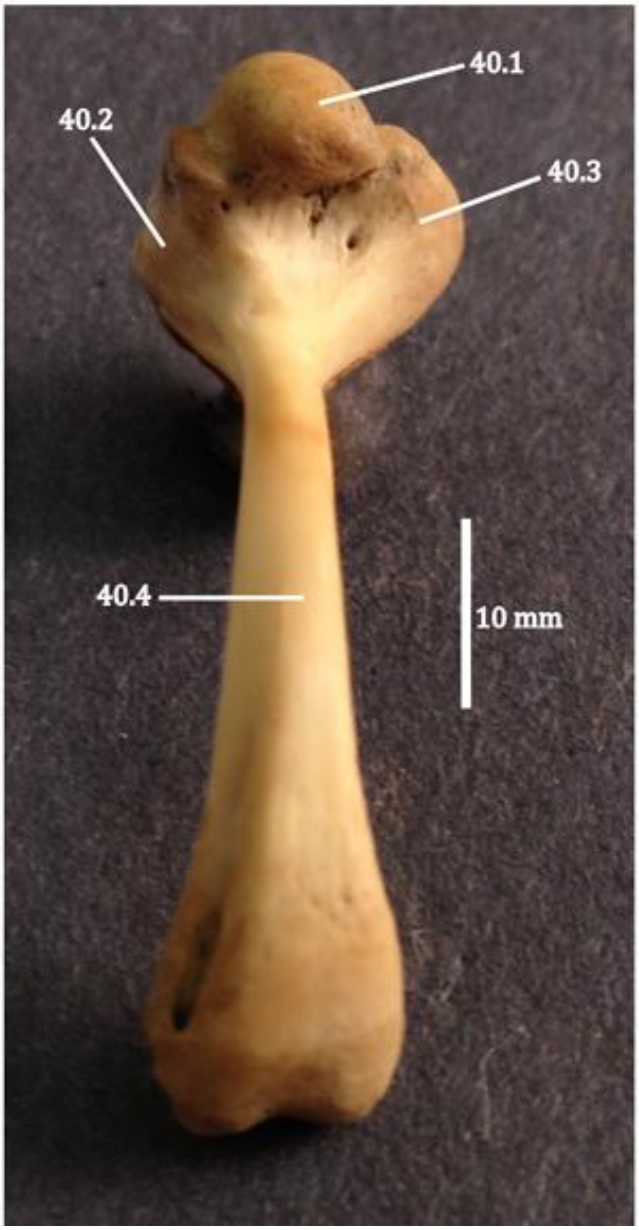

Figure 40: Cranial view of the left humerus of *Emydoidea blandingii* TMM M-9321. 40.1 head of the humerus, 40.2 cranial tuberculum, 40.3 caudal tuberculum, 40.4 corpus.

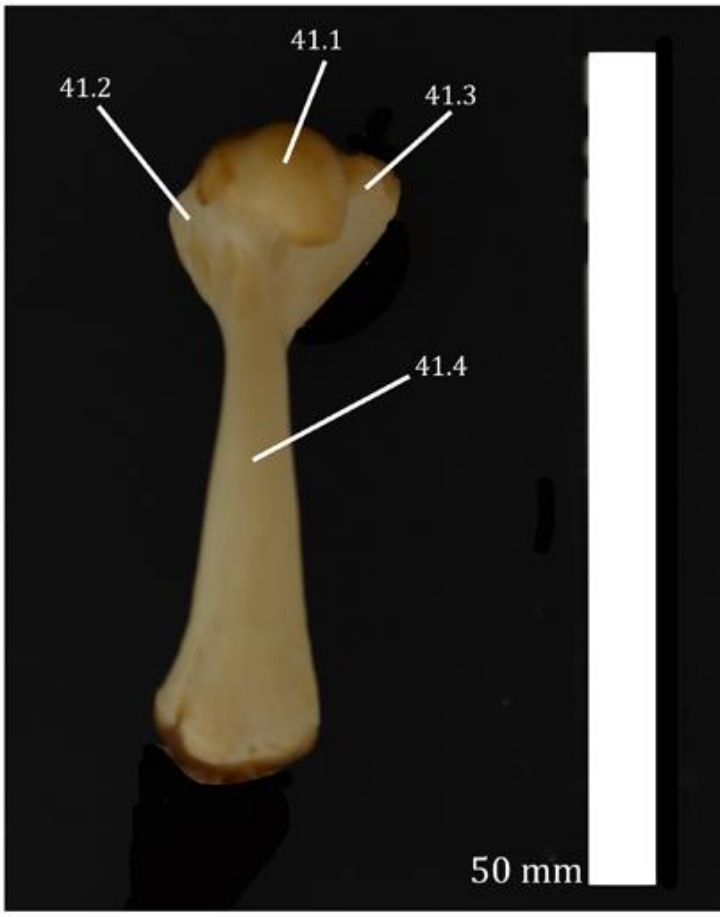

Figure 41: Cranial view of the left humerus of *Terrapene carolina major* CAS 228375. 41.1 head of the humerus, 41.2 cranial tuberculum, 41.3 caudal tuberculum, 41.4 corpus.

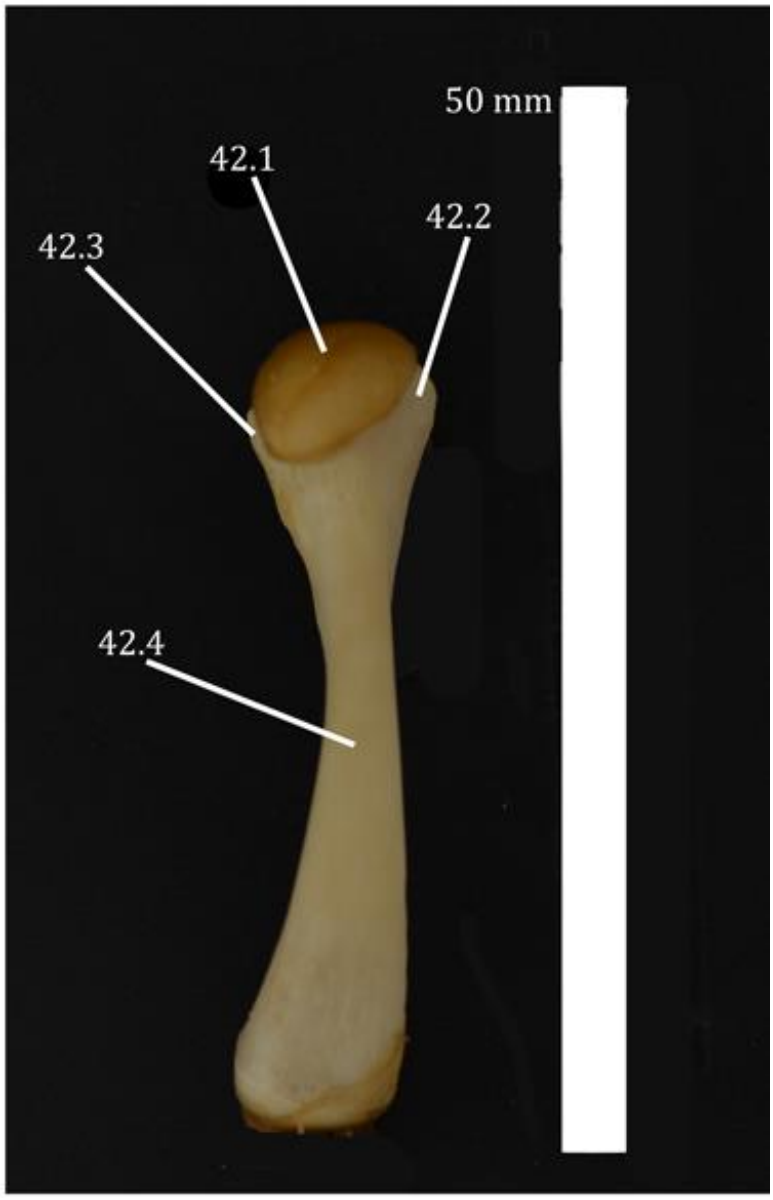

Figure 42: Cranial view of the left femur of *Terrapene carolina major* CAS 228375. 42.1 head of the femur, 42.2 major trochanter, 42.3 minor trochanter, 42.4 corpus.

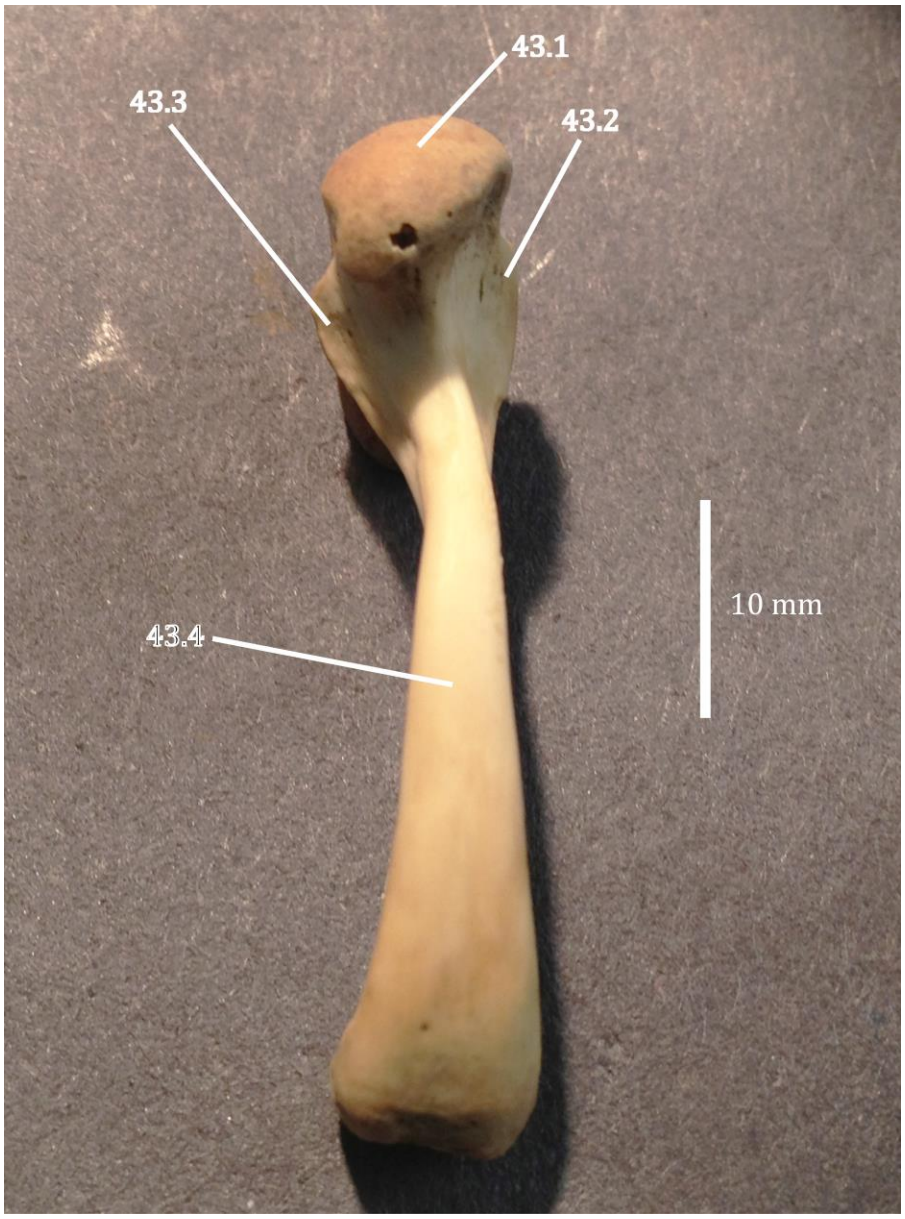

Figure 43: Cranial view of left femur of *Emydoidea blandingii* TMM M-9321. 43.1 head of the femur, 43.2 major trochanter, 43.3 minor trochanter, 43.4 corpus.

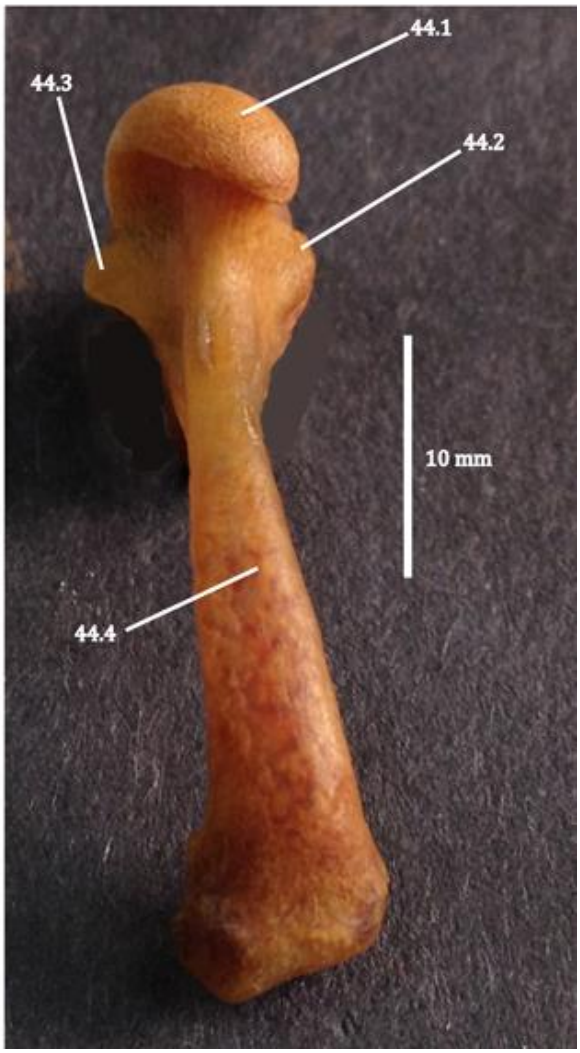

Figure 44: Cranial view of the left humerus of *Emys orbicularis* CAS 228347. 44.1 head of the femur, 44.2 major trochanter, 44.3 minor trochanter, 44.4 corpus.

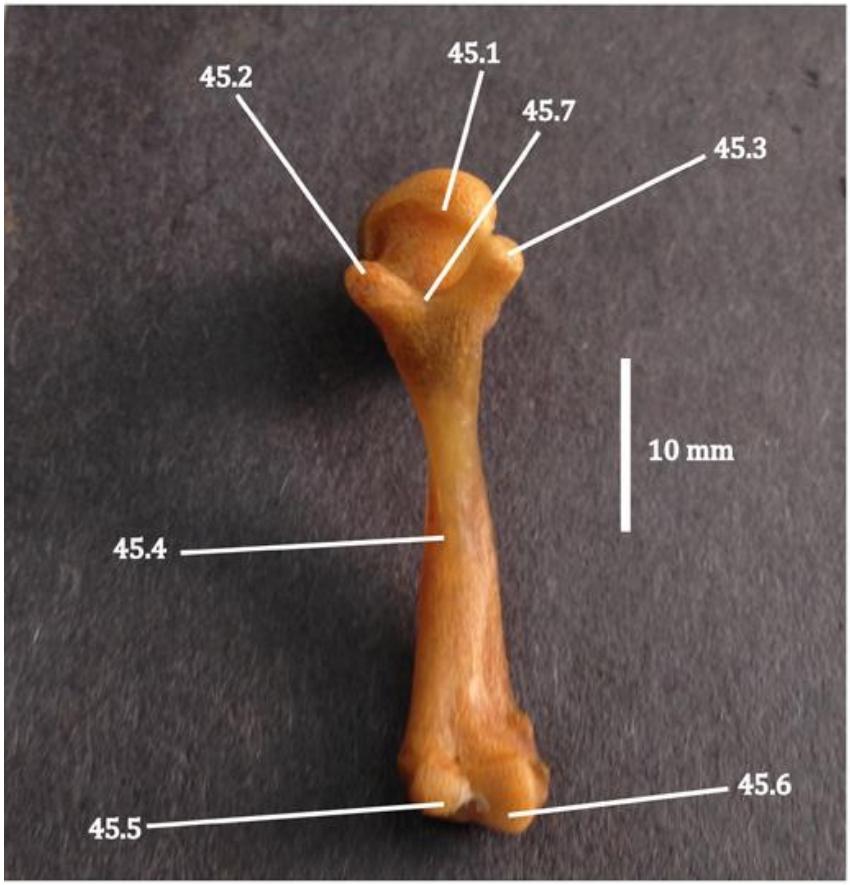

Figure 45: Caudal view of the left femur of *Emys orbicularis* CAS 228347. 45.1 head, 45.2 major trochanter, 45.3 minor trochanter, 45.4 corpus, 45.5 tibial condyle, 45.6 fibular condyle, 45.7 trochanteric fossa.

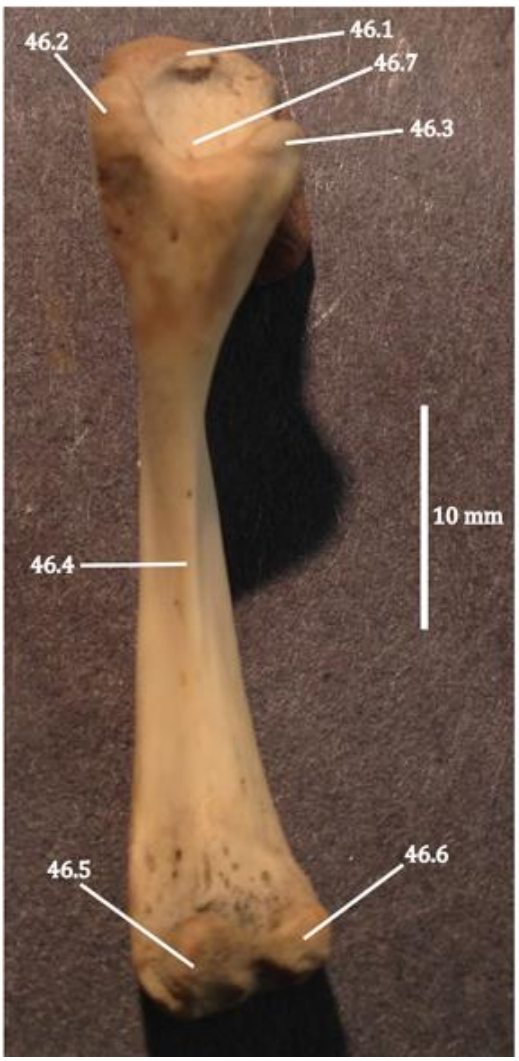

Figure 46: Caudal view of the left femur of *Emydoidea blandingii* TMM M-9321. 46.1 head, 46.2 major trochanter, 46.3 minor trochanter, 46.4 corpus, 46.5 tibial condyle, 46.6 fibular condyle, 46.7 trochanteric fossa.

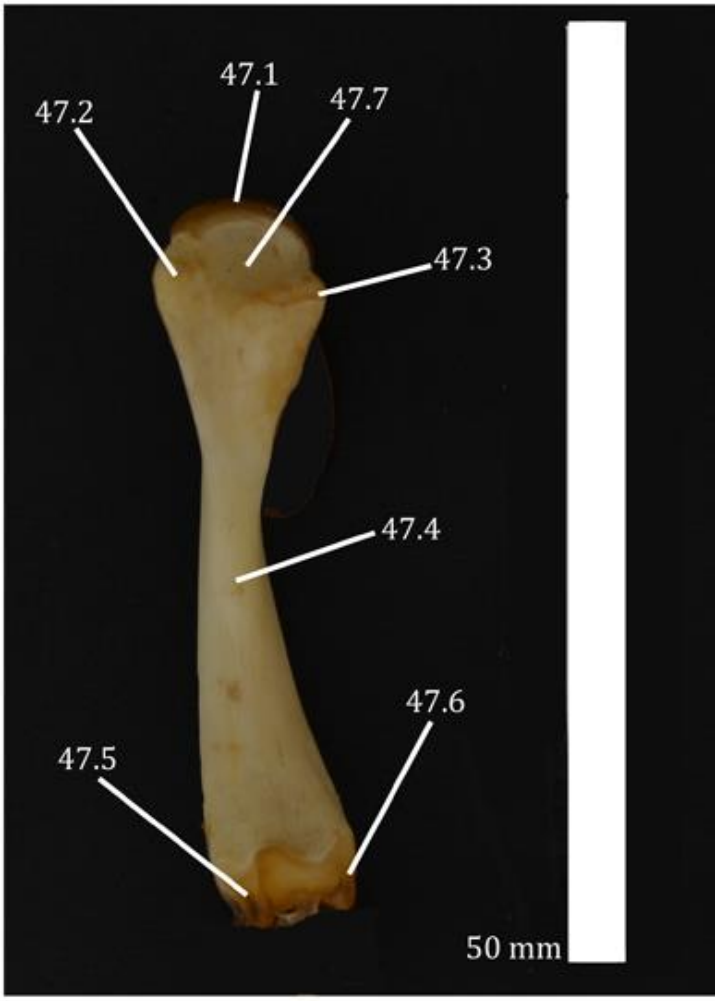

Figure 47: Caudal view of the left femur of *Terrapene carolina major* CAS 228375. 47.1 head, 47.2 major trochanter, 47.3 minor trochanter, 47.4 corpus, 47.5 tibial condyle, 47.6 fibular condyle, 47.7 trochanteric fossa.

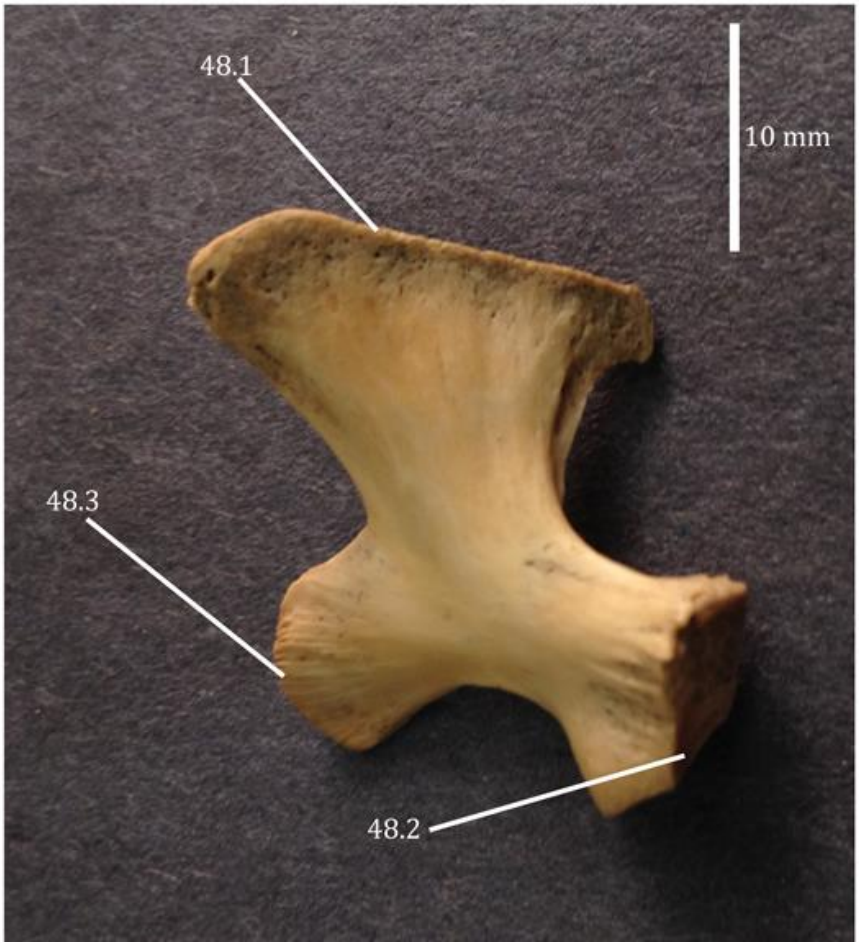

Figure 48: Dorsal view of the left ischium of *Emydoidea blandingii* TMM M-9321. 48.1 ischial-pubic tuberculum, 48.2 acetabular process, 48.3 lateral process of the ischium.

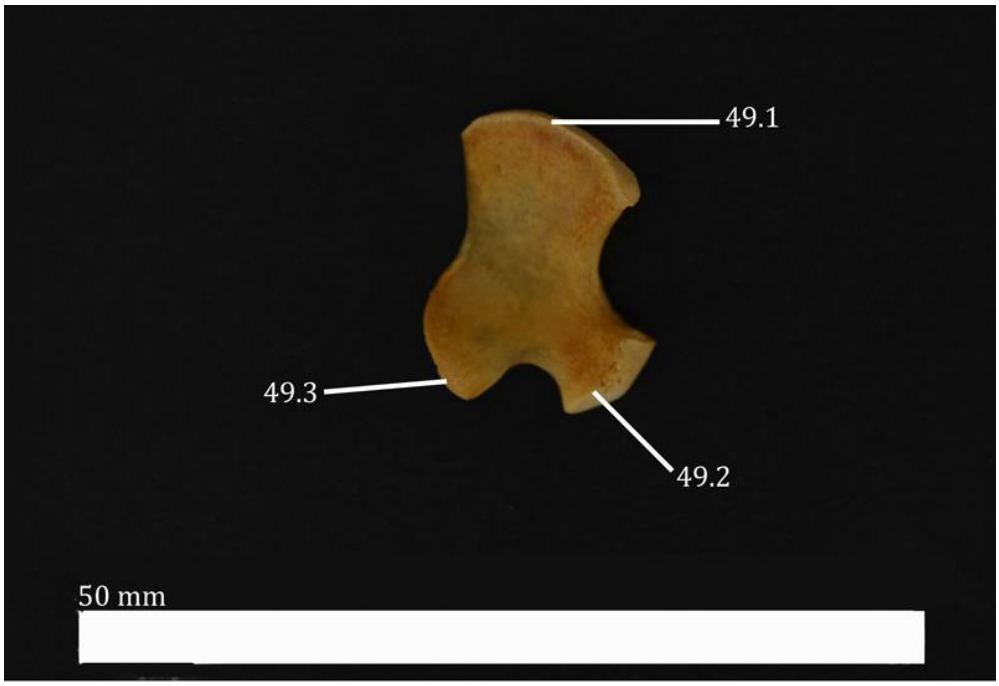

Figure 49: Dorsal view of the left ischium of *Terrapene ornata ornata* TMM M-9881. 49.1 ischial-pubic tuberculum, 49.2 acetabular process, 49.3 lateral process of the ischium.

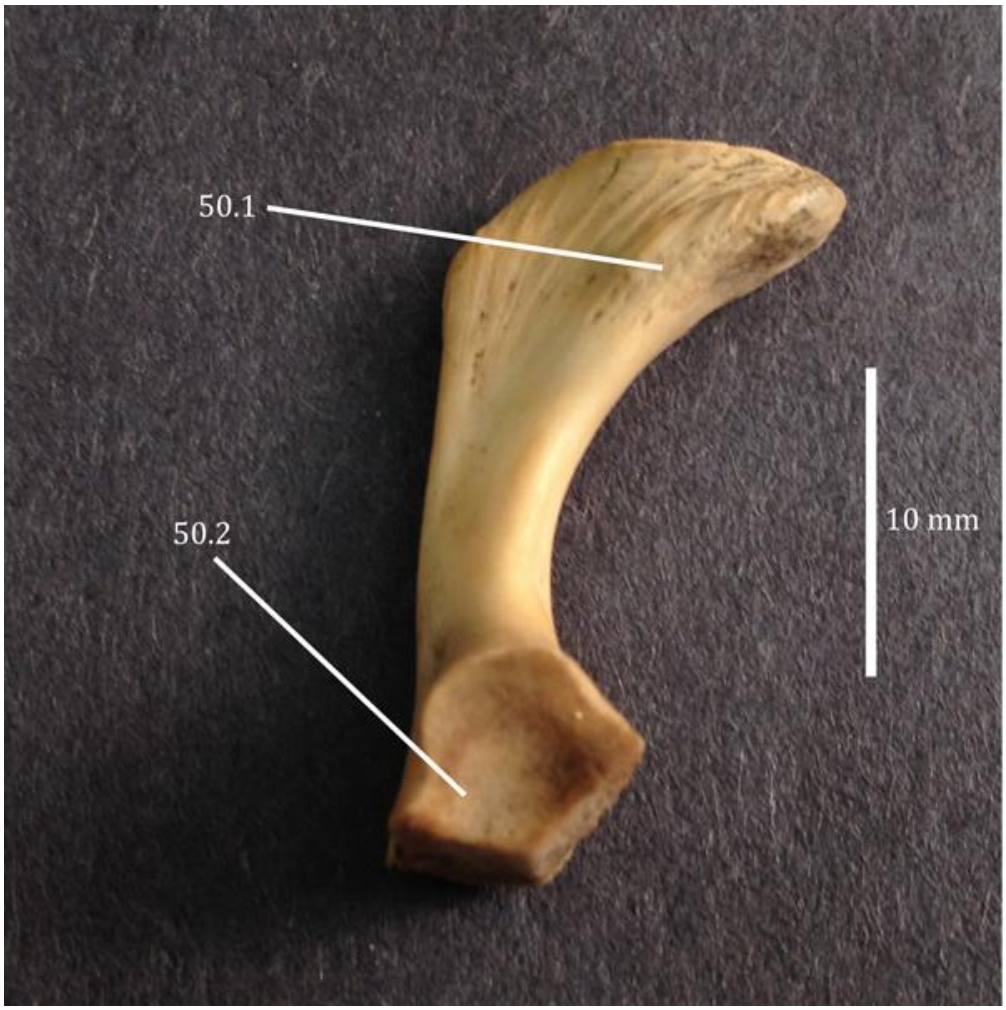

Figure 50: Lateral view of the left illium of *Emydoidea blandingii* TMM M-9321. 50.1 body of the illium, 50.2 acetabulum.

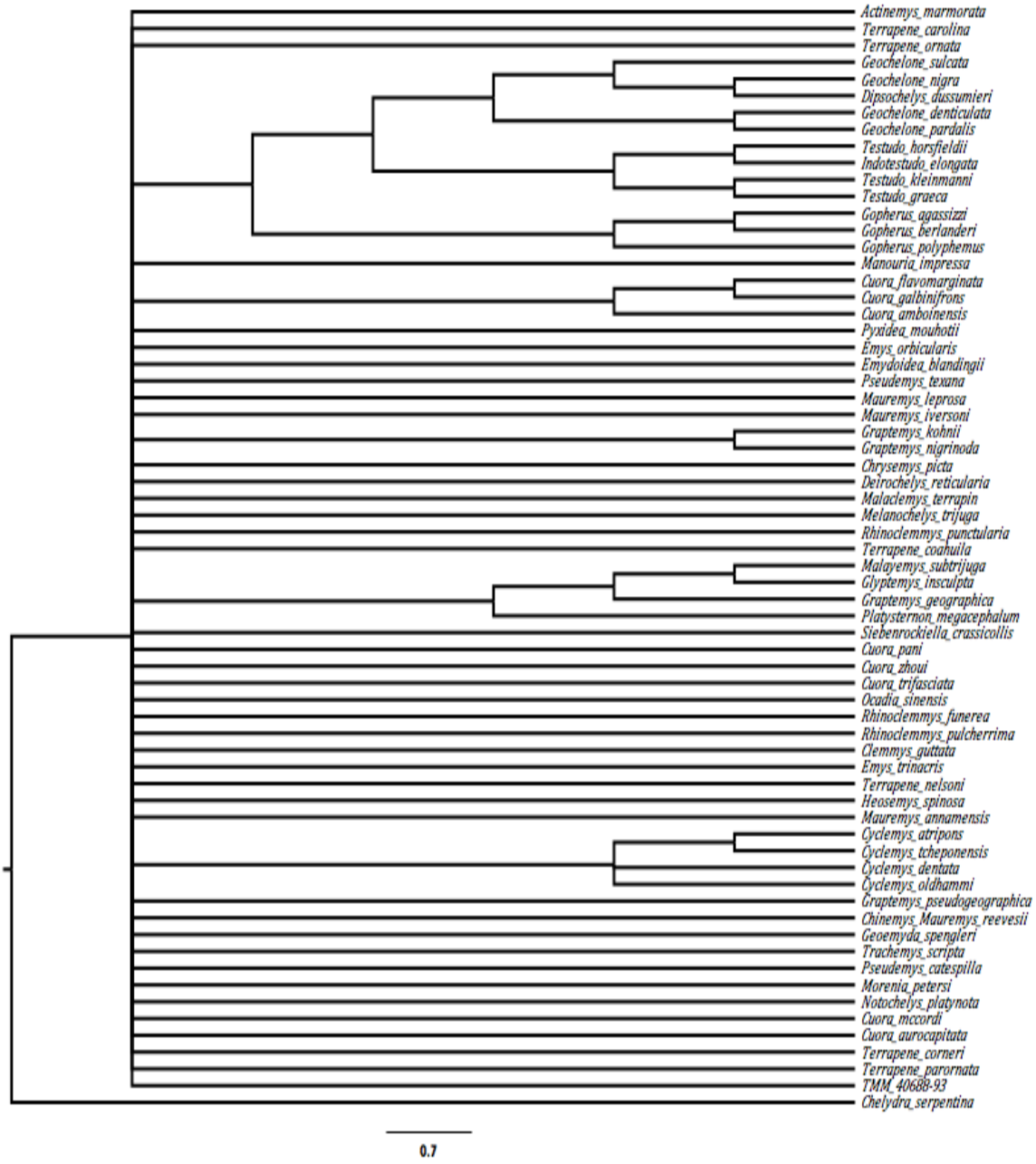

Figure 51: Strict consensus of 10,000 most parsimonious trees of combined morphological and molecular parsimony analysis.

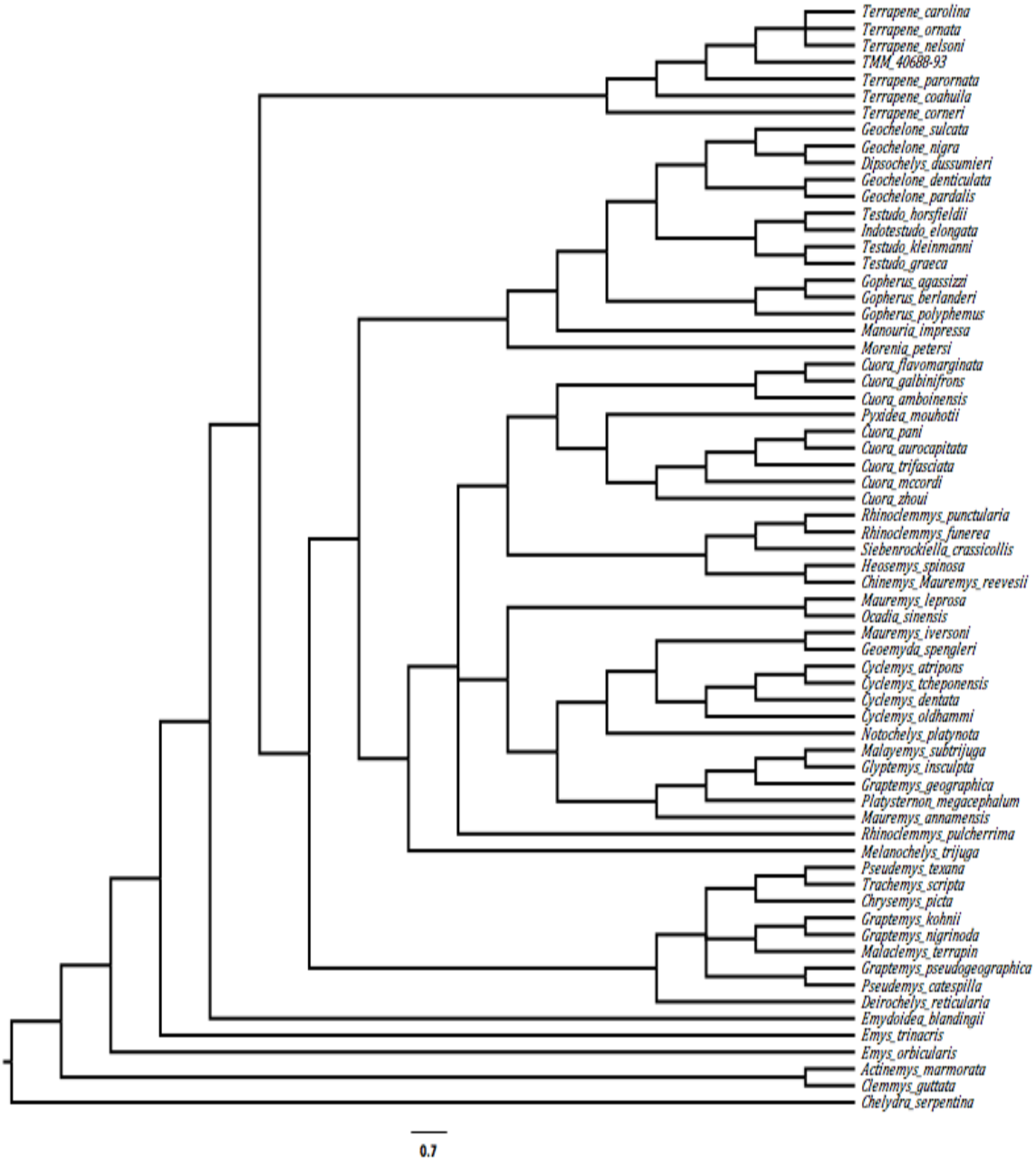

Figure 52: Fifty-percent majority rules consensus tree of 10,000 most parsimonious trees from combined morphological and molecular parsimony analysis.

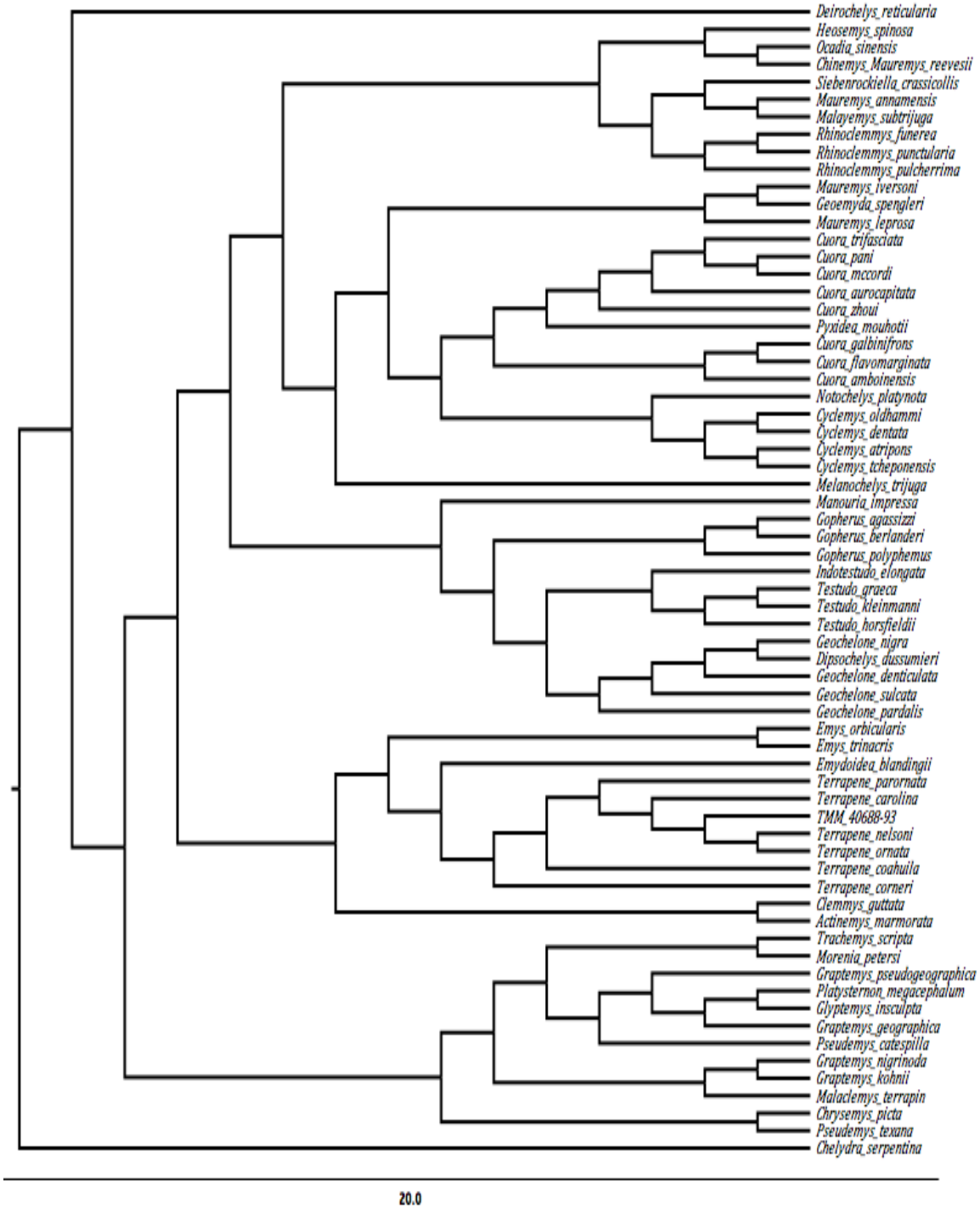

Figure 53: Best tree from maximum-likelihood analysis of morphological and molecular data combined.

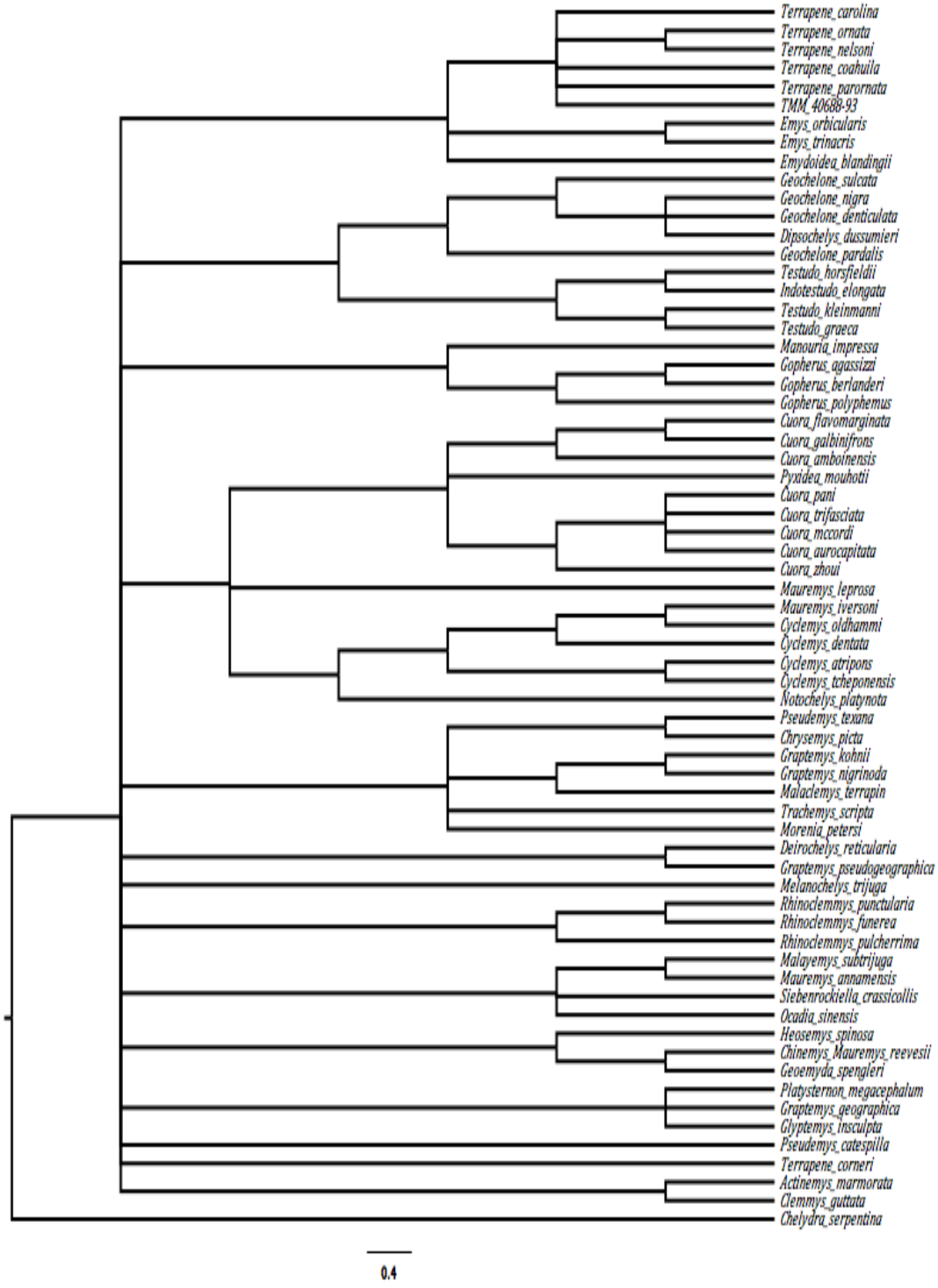

Figure 54: Consensus tree generated from Bayesian analysis of morphological and molecular data combined. Node values are posterior probabilities.


Platysternon_megacephalum_1
Testudo_denticulata_1
Gopherus_agassizii_1
Gopherus_polyphemus_1
Geochelone_nigra_1
Testudo_graeca_1
Geochelone_pardalis_1
Manouria_impressa_1
Dipsochelys_dussumieri_1
Geochelone_sulcata_1
Indotestudo_elongata_1
Indotestudo_elongata_2
Testudo_graeca_2
Testudo_graeca_4
Testudo_graeca_5
Testudo_graeca_3
Gopherus_berlandieri_1
Gopherus_berlandieri_2
Testudo_kleinmanni_1
Testudo_kleinmanni_2
Testudo_kleinmanni_3
Agrionomys_horsfieldii_1
Testudo_horsfieldi_2
Testudo_graeca_6
Testudo_horsfieldii_3
Trachemys_scripta_1
Glyptemys_insculpta_1
Graptemys_geographica_1
Pseudemys_catespilla_1
Malayemys_subtrijuga_1
Malayemys_subtrijuga_2
Malayemys_subtrijuga_3
Malayemys_subtrijuga_4
Graptemys_pseudogeographica_1
Siebenrockiella_crassicollis_1
Rhinoclemmys_funerea_1
Rhinoclemmys_funerea_2
Chinemys_reevesi_1
TMM_40688-93
Terrapene_carolina_1
Terrapene_nelsoni_1
Cuora_flavomarginata_1
Cuora_flavomarginata_2
Terrapene_coahuila_1
Terrapene_coahuila_2
Terrapene_coahuila_3
Terrapene_coahuila_4
Cuora_galbinifrons_3
Terrapene_ornata_1
Terrapene_ornata_2
Terrapene_ornata_3
Terrapene_ornata_4
Terrapene_carolina_2
Terrapene_carolina_3
Terrapene_carolina_4
Terrapene_carolina_5
Terrapene_parornata
Cuora_galbinifrons_1
Cuora_galbinifrons_2
Cuora_amboinensis_3
Chrysemys_picta_1
Deirochelys_reticularia_2
Graptemys_nigrinoda_1

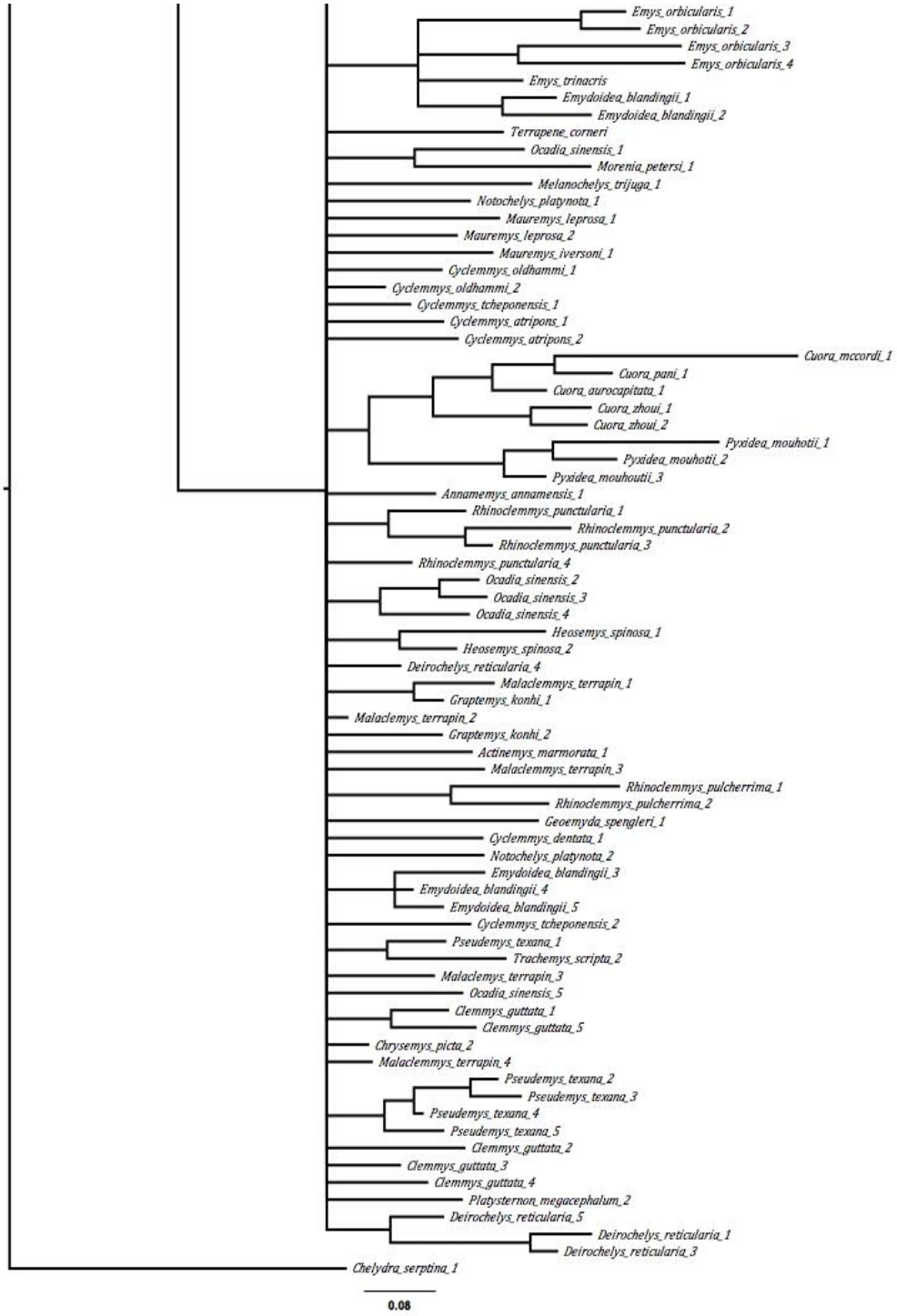

Figure 55: Consensus tree output from Bayesian analysis of individual terminals generated from using only morphological data. Node values are posterior probabilities.

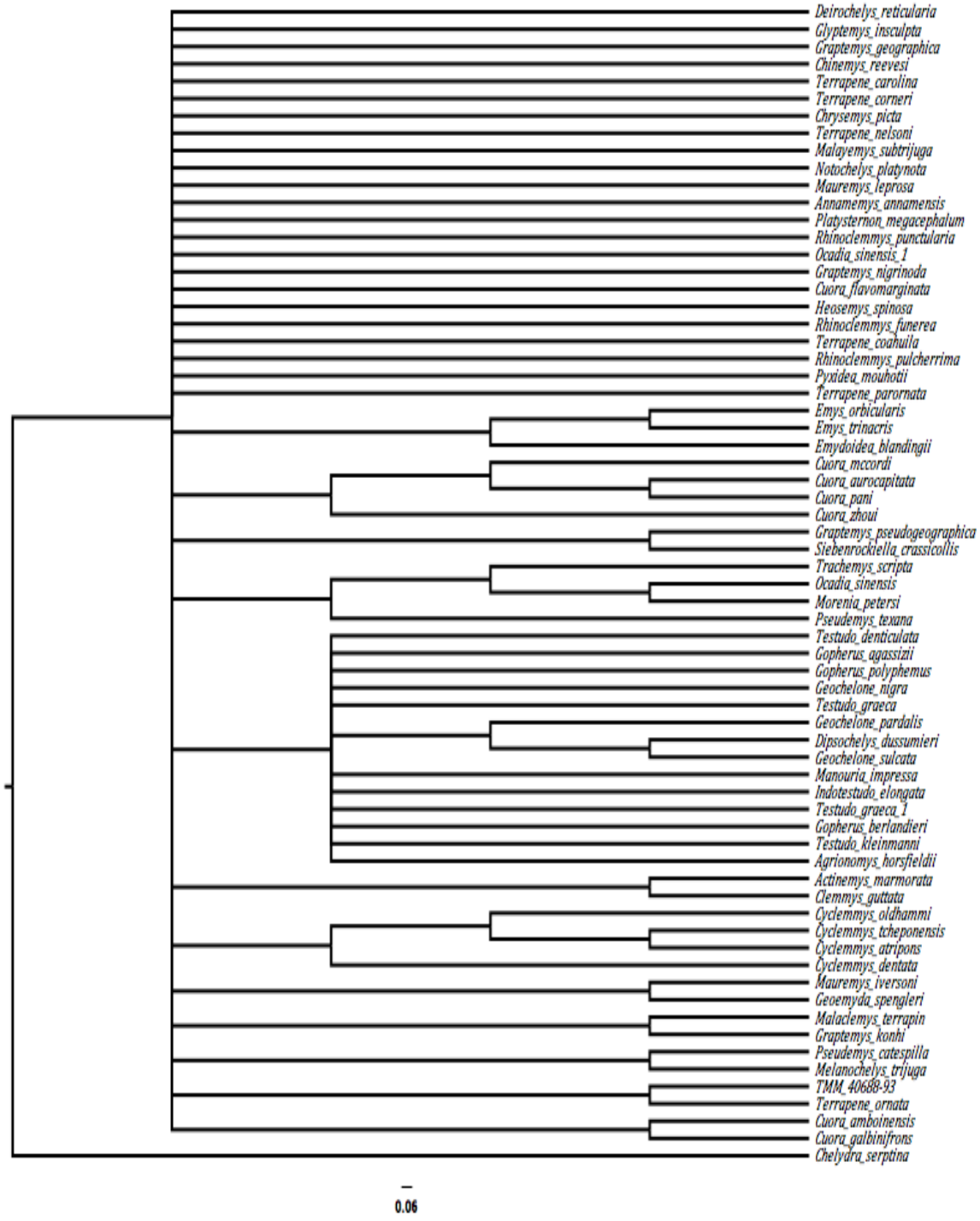

Figure 56: Species-level tree generated from only morphological characters in a Bayesian analysis. Node values are posterior probabilities.

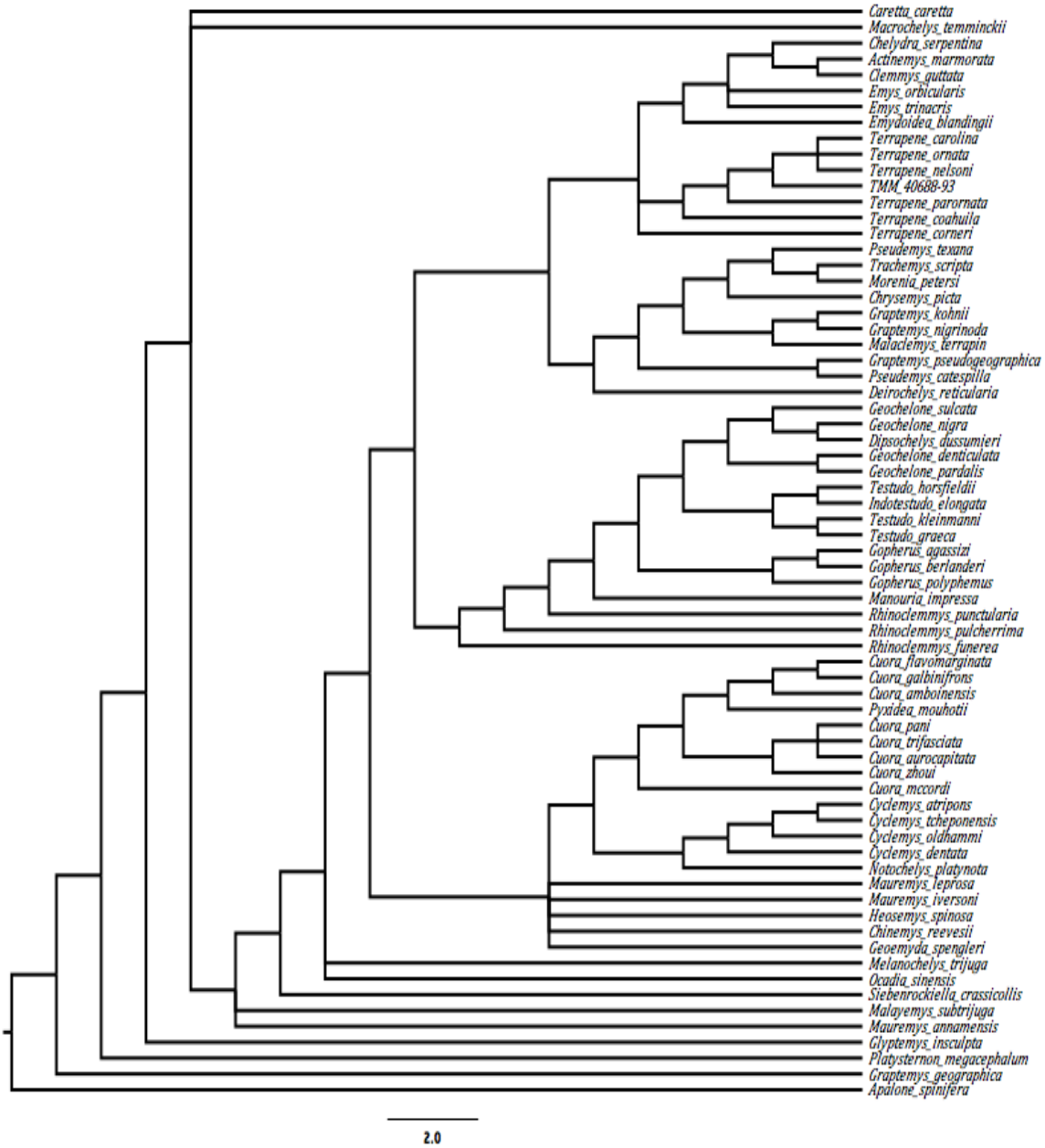

Figure 57: Species-level tree generated from combined morphological and molecular characters in Parsimony analysis, with four additional outgroups.

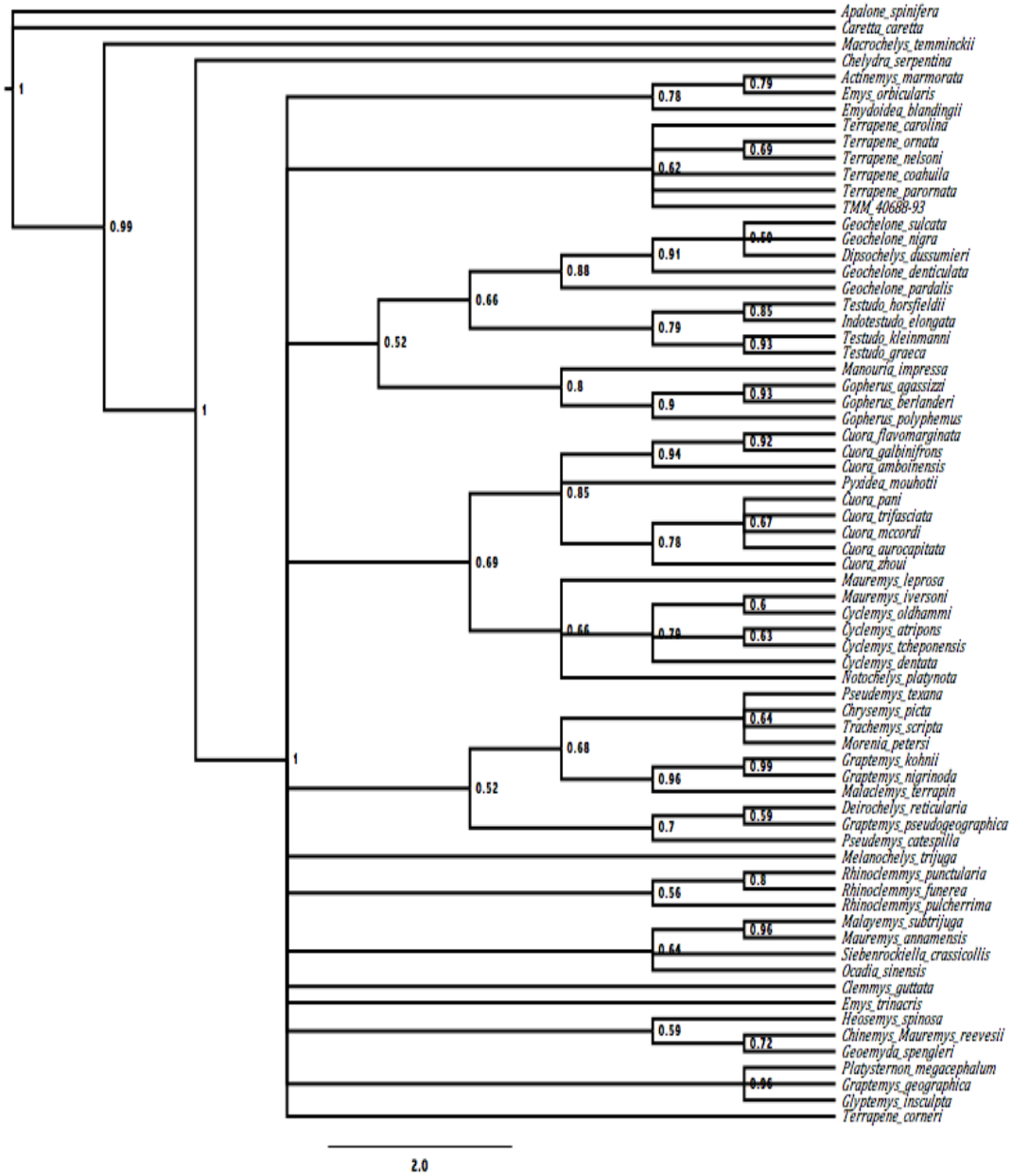

Figure 58: Species-level tree generated from combined morphological and molecular characters in Bayesian analysis. Node values are posterior probabilities.

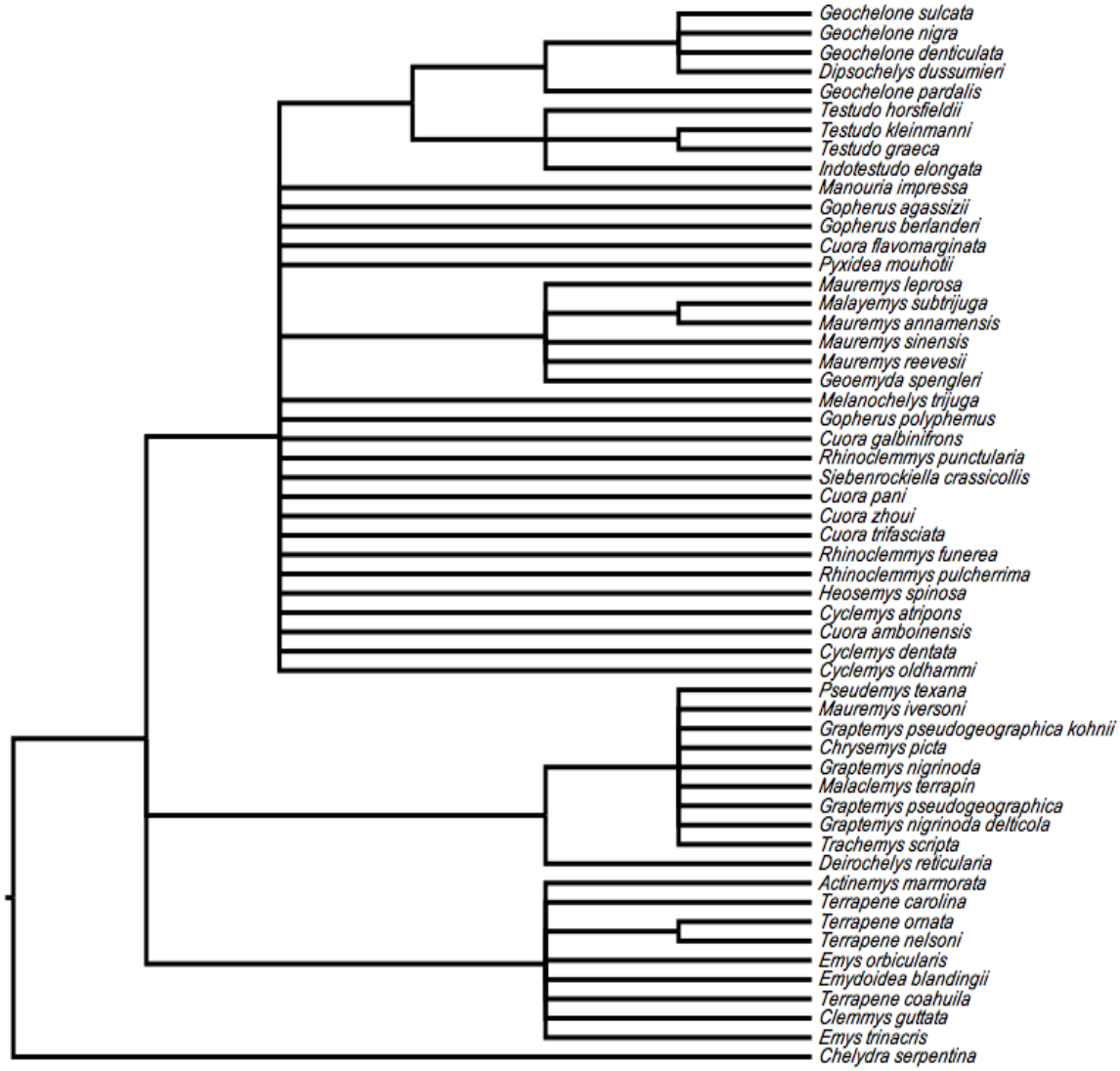

Figure 59: Species-level strict consensus tree of 42,800 most parsimonious trees all three genes.

Chapter 2: Exploring and evaluating the impact of anatomical partitions on morphology-based phylogenetic reconstructions

INTRODUCTION

One of the major problems associated with reconstructing the phylogeny of any group is that ultimately the data available for phylogenetic estimation is limited. This is especially true for representatives of organisms known from fossils. Given that the majority of Life on Earth is extinct and therefore can, at best, be represented only as fossils, it is important to consider the limitations of fossils and the fossil record. In the vast majority of cases, fossils lack complete phenotypic data and virtually all genotypic data for estimating phylogeny. As a result, systematists must use what limited data are available for phylogenetic estimation. But in fact systematists, who work with paleontological or neontological organisms, often self-limit, and use even less data for phylogenetic estimation than what is available. This is because of a historical preponderance towards emphasizing only selected anatomical or genetic regions for phylogenetic estimation. As a result, present researchers in both paleontology and neontology, are faced with a double edged sword; the wealth of data that is represented in 150 years of evolutionary research and observations, and the biases and assumptions that underlay those data and observations.

In order to adequately use pre-existing data and develop new data for use in phylogenetic estimations, systematists must begin to carefully evaluate the biases and

assumptions that affect all biological data. At minimum, we must acknowledge that phylogenetic data are imperfect and incomplete. At best, we can attempt to evaluate and compensate for known biases and assumptions. The field of vertebrate paleobiology represents the area where the limitations of fossil organisms are best realized. It is also a field that has broadly accepted phylogenetic systematics as the dominant mode for developing hypotheses of evolutionary relationships. Virtually all vertebrate groups are actively being studied, but robust vertebrates (i.e., tetrapods) are the ones most likely to be fossilized and found. Among vertebrates commonly found, turtles are almost as ubiquitous in paleontological localities as sedimentary rocks.

Paleontologists working with turtles have largely used two major anatomical regions for describing new turtles represented from fossils: the head or cranial features and the shell, made up of the bony carapace and plastron. The reason for this is that these are the most commonly preserved parts of turtles. A review of literature on recently named fossil turtles, from an arbitrarily chosen year, 2010, illustrates this. *Jiangxichelys* (Tong and Mo 2010) was described from shell material only. *Gamerabaena* (Lyson and Joyce 2010) was described predominantly from skull material with no shell elements preserved. Three species *Cerrejonemys*, *Pacifichelys*, and *Chupacabrachelys* are the only fossil turtles, of seven new taxa, named in 2010, that are known from both skull and shell material (Cadena et al. 2010, Lehman and Wick 2010, and Parham and Pyenson 2010). As a result of these fragmentary specimens, it is important to recognize the limitations on the characters used to identify and describe these fossils and estimate their phylogenetic position.

For instance, in the phylogenetic analysis performed including *Gamerabaena* the character matrix scored consisted entirely of cranial and shell characters (Lyson and Joyce 2010). This underscores the point that paleontologists rely primarily on limited data, but also points to an assumption that has been implicit for morphology-based systematics using turtles; that both turtle shells and skulls each provide complimentary data expected to yield congruent phylogenetic hypotheses. This assumption is critically important, because of the nature of the fossil record of turtles, which is dominantly either shell or skull material and rarely includes fossils with shell data, skull data, and data derived from other anatomical features. In the case of *Gamerabaena* it is described only from skull material, however other baenid turtles included in the phylogenetic analysis are known only from shell material or from both skull and shell material (Lyson and Joyce 2009, Lyson and Joyce 2010). This assumption is pervasive in all forms of morphology-based systematics, and is not restricted to fossil turtles. It is equally common to find fossil mammals described only from teeth or cranial morphology as it is to find fossil snakes described only from disarticulated vertebrae. As such, it is important to understand if disparate anatomical regions provide complimentary phylogenetic signal.

In this study, I address the following question explicitly. Will the morphological characters of the turtle shell (carapace and plastron) and head (cranial osteology and soft tissue), yield congruent phylogenetic hypotheses? The *a priori* null hypothesis tested here would be that these anatomical regions provide congruent estimates of phylogeny independently (in the absence of data from the other region) and serve as complimentary sources of phylogenetic information.

To evaluate this question, I selected a dataset of turtles that are hypothesized to belong to the clade Emydidae. Emydidae is an extant clade of turtles, predominately found in North America, which has been accepted to be monophyletic within most phylogenetic estimations of turtles (e.g., Gaffney and Meylan 1988, Burke et al. 1996, Minx 1996, Shaffer et al. 1997). This clade includes many of the charismatic taxa known to herpetologists and biologists such as *Terrapene*, the extant North American box turtles, *Trachemys*, the ubiquitous North American pond turtles (e.g., sliders), *Pseudemys,* the common North American river turtles, as well as *Emys,* the European pond turtle. Due to the common nature of the turtles, they have been used for many ecological and evolutionary studies (e.g., Legler 1960, Fritz 2003, Bever 2006, Howeth et al. 2008, to name a few). As a result, the phylogeny of the group has become increasingly important as interest has turned towards the conservation biology of the group. Particularly this clade has been studied for its diversification rates, macroevolutionary patterns, end evolutionary rate shifts, patterns of intraspecific variation, and as the fossil record for this group has been better studied, new questions are being asked about its evolutionary history (Bever 2006, Burroughs 2011, Eastman et al. 2011, Vitek and Burroughs 2012, Burroughs et al. 2013). This group therefore is not only interesting for those reasons, but already there exists a robust background of previous research, to facilitate exploration of the proposed head and shell hypothesis discussed above.

To perform this study I modified an already published dataset, that of Wiens et al. (2010), and then conducted a series of tests and analyses to try to determine if two anatomical regions provided congruent phylogenetic hypotheses. The dataset of Wiens et

al. (2010) was originally intended to evaluate discordant phylogenetic hypotheses estimated from mitochondrial DNA or nuclear DNA or both. To evaluate discordance, Wiens et al. used multiple genes to evaluate disparate hypotheses. In addition to the large amount of molecular data used, they also used a large morphological dataset (Wiens et al. 2010). These morphological characters were largely a series of skeletal or soft tissue characters associated with the head or shell or the turtle, many of which had been used by previous researchers (e.g., Gaffney and Meylan 1988, Minx 1996, Shaffer et al. 1997). Because of the characters used and their history, the dataset originally constructed by Wiens et al. (2010) provided and excellent opportunity to further consider signal from distinct anatomical regions.

METHODS

Dataset

The morphological dataset I used is the dataset of Wiens et al. (2010). The dataset from Wiens et al. (2010) has the following history: the bulk of the matrix was generated and scored in Stephens and Wiens (2003) (this the publication provides a detailed list of characters and character states originally used). The dataset had additional characters added to it in Stephens and Wiens (2008). In Wiens et al. 2010 morphological characters in the dataset were rescored following Stephens and Wiens (2008) to allow for their use in Bayesian analyses. The dataset was compiled into a nexus file from the supplemental

material of Wiens et al. (2010) and was analyzed using Mesquite 2.75 (Maddison and Maddison 2011).

To assess the impact of head and shell morphological data separately and together, I modified the dataset of Wiens et al. (2010). I partitioned the dataset into the two anatomical regions and any characters that did not fit within shell (carapace + plastron) or head (osteological + soft tissue head characters) were removed from the analysis. Originally, there were 245 characters in the dataset. I removed 12 characters (characters 234-245) from the dataset that were added by Stephens and Wiens (2008), but lacked character descriptions in that original publication or the supplemental data included in that publication or any subsequent publications (e.g., Wiens et al. 2010). Twenty-eight characters (13, 105-115, 116, 121, 122, 123, and 221 through 233) were removed as these characters were limb and girdle morphology characters and not directly related to cranial or shell characters. Finally, an additional 45 characters (1-12, 84-89, 91, 93, 97, 103, 124-134, 142, 143, 167, 183-188, 209, and 215) were removed. These characters were originally described as a combination of morphometric data or discrete quantities (e.g., the number of suprapygals present). The characters were originally coded in the Stephens and Wiens (2003) matrix, using the frequency-bins (Wiens 1995) and gap-weighting (Thiele 1993) methods. They were subsequently recoded in the Stephens and Wiens (2008) publication in order to be utilized in a Bayesian framework. The characters were rescored following the majority method (Wiens 1995 and Wiens 1999). Stephens and Wiens (2003) wrote that they utilized a frequency-bin method that divided the bins up into character states of A through Y. However there is no description of what

percentage each of these bins makes up in that publication. Stephens and Wiens (2008) seem to presume that future investigators will assume that they have used the A through Y percentage frequency-bin cutoffs used by Wiens (1995), but this is not explicitly stated.

The majority method described by Wiens (1995), is a simple two state character, with 0 being absent, 1 being present. It is however, unclear how frequency-bins were recoded into the one state. Presumably, utilizing the A through Y percent cutoffs of Wiens (1995), all characters exhibiting variation in the A through L range of frequency (0-47%) are clearly demarcated as a 0 (Absent), it is unclear if organisms with the M range of frequency (48-51%) are 0s or 1s (Present). Then one must assume that character states N through Y (51%-100%) are scored as state 1. Discussion of this frequency-bin to majority coding would not only be extremely useful, but is necessary for one to repeat scorings of characters and add taxa to the matrix of Wiens et al. (2010). The gap-weighting method of Thiele (1993) for morphometric characters uses a similar binning approach to frequency-bins, but allows for the weighting of gaps between those bins. Again, in Stephens and Wiens (2003), a description of the series of bins found for morphometric characters is not discussed, and further, in Stephens and Wiens (2008), how these bins were converted to the majority method is unclear. As such, all of these characters were removed due to an inability to faithfully recreate their scorings.

Additionally, I operated under the assumption that the order of the characters in the Wiens et al. (2010) matrix has the same order of the characters described by Stephens and Wiens (2003), I attempted to corroborate this by examining the matrix for characters

with more than two states and determine if they appeared to be in the same position as originally described (e.g., character 172 of Stephens and Wiens (2003) has seven character states, the Wiens et al. (2010) has a character present in position 172 that has up to seven different character states scored).

This parsing of the data resulted in 159 characters. Of these characters, 73 characters were shell related and 86 characters were cranial related. This nearly 50/50 distribution of characters (46/54 to be precise) was critical to avoid limitations when using data partitions for Bayesian analyses. Small partitions can bias results in general, and statistical analysis of Bayesian analyses (i.e., tests of model likelihood like) tend to prefer increased parameterization (Nylander et al. 2004, McGuire et al. 2007). The matrices used for my analyses are found in Appendix 5.

Outgroup selection within Emydid turtles is contentious; *Malayemys subtrijuga* has been utilized by some researchers (e.g., Burke et al. 1996), while others have utilized *Platysternon megacephalum* (e.g., Shaffer et al. 1997). Wiens et al. (2010) utilized *Sternotherus odoratus* as the outgroup within their molecular analyses and ostensibly added *Rhinoclemmys areolata* in morphological analyses (see Wiens et al. (2010) Appendix 6, Supplemental Data), however their published character matrix includes *Sternotherus odoratus* and does not include *Rhinoclemmys areolata* as the only non-emydid taxon. Therefore, their scorings and trees generated with *Rhinoclemmys areolata* are not replicable, based on their published and available data.

The selection of *Sternotherus odoratus* as an independent outgroup is a bit unusual from a morphological point of view. *Sternotherus odoratus* individuals

sometimes possess kinetic plastra, which is a character thought to be derived within the ingroup (e.g., within *Emys, Emydoidea,* and *Terrapene*), they also have a molluscavorious diet shared amongst ingroup taxon *Malaclemmys*, which may result in the polarization of head characters associated with molluscavorious behavior as being primitive. This point was mentioned by Joyce and Bell (2004) as being an additional complication of utilizing *Malaemys subtrijuga* as an outgroup to Emydidae as well.

In some analyses that utilize only cranial data discussed below, *Malaclemmys* comes out as a more basal taxon than it does in the comparison tree. To test for sensitivity in outgroup selection, two outgroup taxa were added to this analyses *Platysternon megacephalum* and *Rhinoclemmys punctularia*. Both lack the cranial characters of *Sternotherus odoratus* and can help determine if character polarization may be biasing resulting tree topology. A series of runs were conducted with and without these added outgroups, and with and without all outgroup taxa being constrained to be more closely related to each other than to the ingroup.

Phylogenetic Reconstruction

All parsimony based reconstructions were performed in PAUP* 4.0B10 (Swofford 2003). All runs were conducted as heuristic searches for 100,000 replicates, with random sequence addition, TBR branch swapping, and branch lengths of zero were collapsed. All characters were not weighted, and all multistate characters were unordered, per the original parameters used by Stephens and Wiens (2003) when the original dataset

was generated and subsequently used by Wiens et al. (2010). Trees from the parsimony analyses are all strict consensus trees. Trees used as figures were generated in FigTree v1.3.1 (Rambaut 2010).

Maximum likelihood based reconstructions were performed in Garli 2.0 (Zwickl 2006). All runs were performed under the implementation of the Mk model (data type=standard) of Lewis (2001), with equal state frequencies, and no invariant sites. It should be noted that the Mk model and the MkV model are only implemented in the 2.0 version of Garli and not in the older releases. For each search, 20 search replicates were performed. At present, there is some debate for the number of search replicates that are appropriate in Garli. The default setting for Garli is five search replicates, however in most cases the best tree (lowest log likelihood tree) was found after the fifth search replicate, but before the tenth search replicate. In all cases the best tree was found within the first 11 search replicates. Trees summarized here are the best trees found by Garli. Again all tree figures were generated using FigTree v1.3.1 (Rambaut 2010).

Bayesian analyses were performed in MrBayes 3.1.2 or MrBayes 3.2.1 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003, Ronquist et al. 2010). All analyses were performed with the Mk model of Lewis (2001) implemented. All analyses were performed under the same parameters prescribed by Wiens et al. (2010) (who used MrBayes 3.1.2): two replicate searches, with four chains, default priors, with samples from each 1000 generations, an additional order of magnitude for total number of generations was added to aid in convergence, for 2.0×10^7 generations. These parameters represent the base parameters, additional partition parameters and outgroup

sensitivity tests were performed using different parameters discussed below. Trees were summarized using the SUMT command and runs were summarized using SUMP command in MrBayes. Convergence was assessed using Tracer v1.4 (Rambaut and Drummond 2007) and confirmed in SUMP. All trees summarized by MrBayes are 50% majority rules consensus trees, and trees figured here were generated by FigTree v1.3.1 (Rambaut 2010).

Dataset Partitioning

I utilized multiple partitioning schemes to compare tree topologies and evaluate their congruency. The comparison of congruency between tree topologies has long represented a standard for assessing phylogenetic accuracy (e.g., Allard and Miyamoto 1991, Miyamoto et al. 1994, Omland 1994, and Cunningham 1997(a)). The idea of congruency is simple, a new tree topology is generated in a phylogenetic analysis, which is comparable to a previous analysis, but has new, more, or different data to inform the new analysis. The new tree topology is compared to the old tree topology and their topological congruency is assessed. If the new topology is congruent with the old topology, the new analysis can be accepted as plausible (Allard and Miyamoto 1991). These analyses are an attempt to discover which (if any) partitioning scheme best compares with the maximum amount of data available, and thus allows investigation of how anatomical regions influence phylogenetic reconstruction and tree topology. For parsimony, maximum likelihood, and Bayesian congruency tests, all runs were conducted

under the parameters discussed above, with exceptions for some Bayesian analyses (discussed below).

Parsimony analyses were conducted with the following datasets to assess congruence. 1) The 159-character dataset was run without data partitioning. 2) The dataset included only cranial characters, by excluding shell characters. 3) The dataset included only shell characters, by excluding cranial characters. Taxonomic was held constant for analyses. In the case where runs failed to complete in a timely fashion (i.e., within 24 hours), runs were stopped and matrices were assessed for cases of taxonomic equivalence (utilizing Select Matching Taxa in Mesquite 2.75), taxonomic equivalents were deleted and runs were re-run utilizing the same parameters. Taxonomic equivalence can prevent a parsimony run from completing, because the relationships between two taxa that are scored the same cannot be resolved (Wilkinson 1995). Each parsimony analyses uses a strict consensus tree to summarize.

Bayesian analyses were undertaken with the same datasets utilized in parsimony analyses, but with additional analyses. Bayesian partition analysis, following the methods of Nylander et al. (2004), was conducted using all 159 characters, with each region partitioned and linked and unlinked parameters were varied. All models tested had an among-site rate variation model formed by an inverse gamma distribution (rates=invgamma). The branch length prior was unconstrained, exponential with a mean of 0.1 (brlenspr=unconstrained:Exp(10)). Two partition models had per-partition rate variation based on an inverse gamma distribution (ratepr=variable). PAUP and Bayes blocks used in these analyses are included in Appendix 6.

Partition Homogeneity or Incongruence Length Difference Test

The partition-homogeneity test (Swofford 2003) or the incongruence length difference test (ILD of Cunningham 1997(b)) is the same test designed to measure the degree of incongruence between two data partitions. ILD is calculated by determining the difference in tree steps in parsimony between non-partition and partitioned analyses. Implementation of ILD is done in PAUP* 4.0b10 (Swofford 2003) as the partition-homogeneity test. The test requires the removal of invariant characters and then the generation of random datasets of equal size to the original. You then evaluate the distribution of ILD p-values and compare with the original ILD to determine if the original dataset has an incongruence value that is greater than would be expected if the dataset were generated randomly. ILD was calculated and then compared with the PAUP* generated ILD values. This was done as a first pass after partitioning the dataset to determine of the partitions of anatomical regions where not dramatically incongruent from one another. As the test requires the removal of invariant characters, three characters were eliminated from the head partition, and eight characters from the shell partition, to assess ILD.

Estimates of Model Likelihood

Among Bayesian partitioning schemes, I ran a selection of linked and unlinked parameters. These can directly or indirectly influence the resulting topology. The methods to estimate the likelihood values and draw comparisons between these models allow for an unprecedented amount of freedom to explore a particular dataset. Clarke and Middleton (2008) utilized a series of Bayesian models to evaluate a hypothesis of evolutionary change in the pectoral and pelvic girdles for fossil birds, they used estimates of model likelihood; which were generated from the log of the harmonic mean after discarding burn-in. Using this method, the harmonic mean estimator of Lartillot and Philippe (2006), model likelihoods can then be converted to Bayes factors and comparison with the best model likelihood (highest model likelihood) and other model likelihoods can be done (Nylander et al. 2004). Bayes factors are compared using the criteria of Kass and Raftery (1995). Several researchers have noted that harmonic mean estimator of model likelihood values have a very high degree of variance, and therefore the resulting preferred model may be biased towards more parameterized models (Lartillot and Philippe 2006, Clarke and Middleton 2008, Xie et al. 2011). To compensate, harmonic mean estimates were run a number of times (up to 1000 times) to determine the average of the harmonic means (Clarke and Middleton 2008). Two more previously proposed methods of estimating model likelihood have been proposed to be more accurate than the harmonic mean estimator; thermodynamic integration of Lartillot and Philippe (2006) and stepping-stone sampling of Xie et al. (2011). Each method is more computationally intensive than harmonic mean estimation, but stepping-stone sampling (SS) is significantly less intensive than thermodynamic integration and allows

for rapid estimations of model likelihood. Stepping-stone sampling is implemented in MrBayes 3.2.1 (Ronquist et al. 2010), Phycas 1.2.0 (Phycas Development Team 2010), and Beast v1.7.4 (Drummond et al. In Press). However, within Phycas the Mk model of evolution (Lewis 2001), which models the evolution of morphological characters in a maximum likelihood and Bayesian framework is not implemented, and therefore steppingstone sampling in Phycas cannot be used with morphological data. I utilized the stepping-stone sampling algorithm that is implemented in MrBayes.

Stepping-stone sampling while simple to implement in MrBayes, appears to have some computational limitations. When running SS for many generations (> 2 x 10^6 generations), some runs slowed down tremendously and would not converge. To test why, I ran a series of tests discussed below in "Troubleshooting Stepping-Stone". The number of stepping-stone generations was limited to 1.5 x 10^6 generations, as all runs tested would reach convergence within this number of generations. Estimates of model likelihood are summarized in the results below.

Troubleshooting Stepping-Stone

The SS method samples across both the prior and posterior distributions within a Bayesian run. When a particular dataset is small and the number of steps sampled is sufficiently large, the sampled step may be in a section in which the prior and posterior distributions are very close and moving towards the tail of the distribution, which is an exponential asymptote going towards negative infinity. When this occurs the ability of

stepping-stone sampling to converge on a value that represents the mean, is no longer there. Because of this SS takes an exponentially long time to converge on a value, and will in fact never converge. The solution to this problem is relatively simple one utilizes an SS run that has fewer and thus wider steps across the distribution.

To confirm that utilizing fewer steps over more steps still provides a reasonable estimate of model likelihood, I ran a dataset through SS utilizing different values for the number of generations that SS ran. I ran the same dataset, one with outgroups added, an outgroup constraint, with all characters in a single partition, through different values of SS generations for a total of 6 runs. I started with the default 2.5×10^5 generations, then 5×10^5, 7.5×10^5, 1×10^6, 1.5×10^6, and finally 2×10^6. All runs except the one of 2×10^6 generations converged. The variance from across those generation values was extremely low, 3.34 log likelihood values, this represents approximately 0.001% of the mean of the five values for converged runs. This low variance indicates that utilizing fewer generations in SS does not impact the resulting estimations. The number of steps required to reach non-convergence varies from dataset to dataset depending on the priors and how they shape the prior and resulting posterior distributions.

RESULTS

Partition Homogeneity or Incongruence Length Difference Test

The results of the incongruence length difference test were ambiguous. Under the partition-homogeneity test, the measured difference was a p-value = 0.01. There have

been multiple interpretations about which p-values are and are not statistically significant (for a review see: Cunningham 1997(b)). The generally accepted cut off is that when p-values are greater than 0.01, there is significant incongruence between data partitions and the partitions should not be combined in an analysis, while values less than 0.01 have more congruence than incongruence and can be combined (Cunningham 1997(b) and Lee 2001).

Parsimony Analyses

Comparison of the consistency index (CI) between trees derived using the same taxa but different datasets in parsimony, has been suggested to be a way in which a character set can be viewed as better (Archie 1989). Consistency index values range from 0 to 1, with 0 being a dataset that has characters that are all homoplasious and 1 being a dataset free of homoplasy. The general consensus for CI comparisons is that if a particular dataset has a CI closer to 1 than another data, then it is viewed as more consistent and is therefore the better dataset (Kraus 1988). In this case the two CIs from the head data and shell data are very comparable. I generated the CI for each dataset on the comparison tree topology. The dataset made up of head characters has a CI of 0.3131 and the dataset made up of shell characters has a CI of 0.2901.

A list of analyses run under parsimony is provided in Table 2. In that table, the main metric of comparison is that of number of clades shared (NCS). Number of clades shared is an approximate metric for congruency between two trees. In the case of the data

here, NCS is measured between the comparison tree (the tree generated using all of the morphological data) and the disparate trees generated using either head or shell characters. If trees are 100% congruent NCS will be identical, but if there is increased or decreased resolution with respect to the comparison tree NCS is different. NCS is a measure of monophyletic clades; polytomies do not count. There are cases in which a polytomy exists in a resulting tree that did not exist in the comparison tree, so NCS between the two are not the same. However, it may be the case that tree topologies are consistent with one another, despite not having equal numbers of clades, because polytomies can be consistent with monophyly but do not demonstrate it. An additional metric contained in Tables 2b is "Clades Shared with Comparison Tree," this is different from the number of clades shared, in that it provides a list of the actual clades with the same taxa contained within them shared between the comparison tree and the tree being compared. I also note whether a specific clade is present, clades are numbered in the comparison tree (Figure 60) and denoted if present in the tree being compared with an X. Some topologies are referenced in the discussion below, all other tree topologies generated from all analyses are figured in Appendix 7.

Maximum Likelihood Analyses

Results from maximum likelihood reconstruction were consistent with the results from Bayesian analyses. For this reason, the resulting tree topologies are provided in

Appendix 7, but summarizing the results would be redundant with the Bayesian summary provided below.

Bayesian Analyses

A list of analyses run using Bayesian methods is provided (Table 3), along with the number of partitions, among-partition rate-variation model, model likelihood values estimated from Stepping-Stone, Bayes factor comparisons, the total number of monophyletic clades in the resulting tree, the number of clades shared with the comparison tree, and whether or not clades 1-29 of the comparison tree (Figure 61) are present in the tree being compared (X denotes present).

For Bayesian analyses, I compared three sets of five potential models, with different outgroups and/or the addition of an outgroup constraint. In all cases the preferred models were those that separated anatomical regions into their own partitions. However, depending on the additional taxa or dataset constraint, different among-partition models were preferred. All models tested had an among-site rate variation model of invariable-site-gamma (rates=invgamma) and the branch length prior was an unconstrained, exponential, with a mean of 0.1 (brlenspr=unconstrained:Exp(10)). Invgamma allows for a proportion of the sites in the dataset to be held as invariable, and then draws the remaining portion of the variable sites from a gamma distribution. A standard gamma rate model stipulates that all sites be variable. My choice of invariable-site-gamma rate variation model was driven by the presence of known invariable

characters in the dataset. All two partition models had per-partition rate variation based on an invariable gamma distribution.

DISCUSSION

In the initial investigation of whether or not head characters and shell characters yield congruent topologies, the answer at first seems to be that they do not. Head characters and shell characters do not yield *wholly* congruent topologies. However, there is some congruence between shell and head data and when they are combined there is certainly a higher level of congruence with the comparison hypotheses (generated using all 245 morphological characters), which are assumed to represent the best estimate of phylogeny. In the case of no, the question immediately becomes why are the hypotheses of relationships not congruent?

One potential reason for dataset incongruency is due to character conflict. Here, I used ILD to attempt to assess if these partitions were sufficiently conflicting that they should not be combined to estimate phylogeny. The results of ILD are ambiguous, but if the datasets were largely congruent with one another, ILD results should support their combination. If, conversely, they were largely incongruent ILD should support their separation. In this case neither condition applies, suggesting that the phylogenetic signal of the datasets is incongruent, but not wholly in conflict.

Another potential way of assessing whether one anatomical region may have more congruent phylogenetic signal is the comparison of consistency index scores. In this case, comparison of CIs is not informative about which dataset may yield stronger

phylogenetic signal. The scores are close to each other and they closer to 0 than they are to 1. This suggests that in both datasets there is a relatively high degree of homoplasy, but their CIs are sufficiently close that neither one would be preferred for phylogenetic estimation.

I chose as my preferred model the model that was estimated using the dataset with two additional outgroups and with the outgroup constraint. This model is preferred by 506.1 Bayes factors, when compared with other models generated using the same parameters. This model has two anatomical partitions, with branch lengths unlinked, but with topology linked (Figure 62). I chose this model because it shares the largest number of clades with the comparison tree (Figure 61) and was the most resolved tree of my Bayesian analyses (clades shared summarized in Table 3a-d). When no additional outgroups were used, a model that partitioned by anatomical region, with branch lengths and topology linked was strongly preferred. When additional outgroups were included, a model that partitioned by anatomical regions, with branch lengths linked, and unlinked topology was strongly preferred.

The preference of a model with unlinked branch lengths in all three dataset permutations may reflect a difference in evolutionary rates between the two anatomical regions. Branch lengths have been proposed to be proxies for evolutionary rate when evaluated on a phylogeny (McGuire 2007, Clarke and Middleton 2008). In this case, a model preferring unlinked branch lengths may suggest that there is rate heterogeneity between the head and shell of emydid turtles. This is in line with findings recently proposed supporting a rate shift in the evolution of mean body size for emydid turtles

sometime during the Tertiary (Jaffe et al. 2011). This may suggest that the discrete characters in this analysis capture a similar signal, potentially reinforcing these findings. However, further investigation of this potential rate shift is required.

The analyses of truncated datasets (i.e., head or shell only) conducted here recovered some clades more consistently than others. Historically, the Emydidae was proposed to have two distinct clades, the Emydinae and the Deirochelyinae (Gaffney and Meylan 1988). The analysis by Gaffney and Meylan represented a benchmark by which subsequent analyses were compared. Those later analyses focused on most of the same characters and also tended to recover a monophyletic Emydinae as the sister taxon to a monophyletic Deirochelyinae (e.g., Shaffer et al. 1997, Stephens and Wiens 2003, Stephens and Wiens 2008, and Wiens et al. 2010). That traditionally proposed relationship was recovered in my Bayesian comparison analysis of all characters (Figure 61: Clade 1 is the Deirochelyinae and Clade 21 is the Emydinae). However, once the number of characters in the dataset is reduced, this sister relationship is no longer recovered. In fact, in my analyses the Deirochelyinae is frequently not recovered (recovered in only four of 21 Bayesian analyses). The Emydinae is recovered more often (16 of 21 Bayesian analyses).

The monophyly of the traditionally recognized Deirochelyinae is sensitive to outgroup selection. The Deirochelyinae is recovered most in analyses with added outgroup taxa. This is because *Malaclemmys* is traditionally recognized as a deirochelyine turtle its hypothesized relationships move when using *Sternotherus odoratus* as an outgroup. However, the Deirochelyinae still not recovered in seven of the

ten Bayesian analyses run with additional outgroups. This is reinforced by the fact that Wiens et al. (2010) consistently recovered the Deirochelyinae using large amounts of molecular data.

The monophyly of *Terrapene* has long been assumed among researchers who have worked on the taxon (e.g., White 1929, Milstead 1969, Minx 1996). However, the appropriateness of this assumption has not been tested. Although my analyses did not set out to evaluate the monophyly of *Terrapene*, the clade is consistently recovered (Clade 7 in parsimony analyses and Clade 26 in Bayesian analyses), often to the exclusion of other relationships. It appears that there are sets of characters contained both within the head and shell region of *Terrapene* that can readily identify its members as a monophyletic group with respect to all other emydids. The consistent recovery of *Terrapene* as monophyletic based on genetic data also reinforces this (Stephens and Wiens 2003, Stephens and Wiens 2008, Wiens et al. 2010, Burroughs; Chapter 1 of this thesis).

There are multiple other clades that were recovered in the majority of parsimony or Bayesian analyses. Clade 4 of the parsimony analysis contains all taxa of *Terrapene*, both species of *Glyptemys*, and *Actinemys marmorata*, all of which are taxa traditionally assigned to the Emydinae, but the relationships between these taxa were not previously recovered by other researchers (e.g., Gaffney and Meylan 1988, Shaffer et al. 1997, Wiens et al. 2010). Clade 5 of the parsimony analysis is a clade containing both species of *Glyptemys* and all taxa of *Terrapene*. The consistent recovery of Clades 4, 5, and 7 indicates strong morphological support for a shared relationship between *Glyptemys, Terrapene*, and *Actinemys*. Clades 9 and 10 are associated with relationships contained

within *Terrapene*, and both support the non-monophyly of *Terrapene carolina*. Non-monophyly of *Terrapene carolina* seems probable given recent genetic research showing reticulation and introgression between *Terrapene carolina* and *Terrapene ornata* (Martin et al. 2013). Researchers working with Pleistocene fossils and modern specimens of *Terrapene carolina* recently noted that it is easy to conflate specimens of *Terrapene ornata* and *Terrapene carolina* because neither has a robust morphological diagnosis (Vitek and Burroughs 2012). Clade 31 in the parsimony analysis also is consistently recovered. It comprises the sister taxa, *Graptemys gibbonsi* and *Graptemys pulchra*; an exhaustive phylogenetic analysis of the species of *Graptemys* has not been performed to date. This relationship was not consistently recovered by the analyses of Wiens et al. (2010) based on molecular data.

In the Bayesian analyses Clade 5 and Clade 6 represent the relationshps; between *Pseudemys peninsularis, Pseudemys rubriventris,* and *Pseudemys nelsoni*. The sister relationship between *Pseudemys rubriventris* and *Pseudemys nelsoni* was recovered by Wiens et al. (2010) in some of their analyses. But the Clade 5 relationship was not consistently recovered. A recent attempt to evaluate sister relationships among species of *Pseudemys* resulting in the suggestion that there are multiple species currently named in that genus that may not represent real species (Spinks et al. 2013). Clades 15 and 16 reflect relationships between *Graptemys nigrinoda, Graptemys oculifera*, and *Graptemys flavimaculata*, the relationships in clade 16 were not recovered by Wiens et al. (2010), but different relationships with the same taxa found in clade 15 were recovered in their analyses. Clade 19 represents the same set of relationships as Clade 31 in the parsimony

analyses. Clade 24 represents the same set of relationships as found in clade 5 of the parsimony analyses.

CONCLUSIONS

My results do not support the idea that head and shell characters can be used independently to derive congruent phylogenetic hypotheses. Because the two anatomical regions do reflect the same evolutionary histories, the next logical questions are whether it is reasonable to combine the partitions or whether one anatomical region is better for estimating phylogeny over another. In attempts to address these questions I used ILD, comparison of CI scores, and Bayesian model comparisons.

The ILD results were ambiguous, neither supporting nor rejecting the idea that head and shell data could be combined. Comparison of CI also was ambiguous, because neither dataset was clearly preferred as being more consistent and both seem to have a high level of homoplasy. Yet, this comparison allows for a careful evaluation of both datasets to determine if there is a reason to use one dataset over another. In this case there is not. The combined ILD and CI comparisons only serve as justification for continued exploration. In other cases, however, they may provide definitive answers to whether or not data should be combined, or if one anatomical region would be preferred. In the case of emydid turtles, CI comparisons indicate that there is no *a priori* reason to prefer shells to heads or vice versa, contrary to what has been proposed in the past (i.e., Gaffney 1975). In fact, CI comparison and ILD ambiguity reinforce the hypothesis that with respect to Emydidae neither dataset gives the whole and complete picture with respect to

phylogeny. That notion is further underscored by the results of the Bayesian model comparisons.

From simple topological comparison it is clear that shell-only and head-only datasets do not yield the same hypotheses of relationships. The Bayesian model chosen for these datasets reinforces the idea that each region should be combined. But my results support the idea that the evolution of this group may be best modeled with some degree of independence between anatomical regions, as opposed to a minimal evolution model. In doing this, researchers may more closely approximate the complexity of the evolutionary history of this group and may arrive at better estimates of phylogeny.

With respect to Bayesian model-likelihood estimates via SS, it is also important to note that the models selected by SS were not the most parameterized models. This is important because many previous researchers have noted the tendency of estimates made via the harmonic-mean estimator to preferentially choose more parameterized models (Nylander et al. 2004, McGuire et al. 2007, Lartillot and Philippe 2006, and Xie et al. 2011). In this case in using SS, the most parameterized model (e.g., the one with topology and branch lengths both unlinked), was never the preferred model. Although more parameterized models were chosen over the least parameterized model (e.g., the single partition model), the choice of less parameterized models over the most parameterized lends credence to the model selected via SS. All preferred models were partitioned by anatomical region, a result that has previously only been reported by Clarke and Middleton (2008). For future researchers, this is another important test for SS and model-selection using this method.

The consistent recovery of certain clades within analyses is important for understanding the state of relationships within Emydidae. The consistent recovery of the Emydinae and *Terrapene*, help support previous assumptions of their monophyly. However, the inconsistent recovery of monophyletic genera (in particular *Trachemys, Graptemys, and Pseudemys*) and the Deirochelyinae only serve to undermine previous assumptions of monophyly. Most previous studies focused only on sub-sections of the Emydidae or used relatively small taxonomic samples (i.e., Minx 1996, Burke et al. 1996, Shaffer et al. 1997). Studies that used larger taxonomic samples often were inconsistent in recovering the monophyly of traditional clades or maintaining traditional sister taxon relationships (e.g., Wiens et al. 2010, Thomson and Shaffer 2010, Spinks et al. 2013).

The decrease in phylogenetic resolution seen here is almost certainly a result of the reduced number of characters in my datasets as compared to Wiens et al. (2010). However, if researchers want to evaluate *fossils* for their phylogenetic affinities to delve deeper (chronologically) into the history of groups, good resolution and confidence in the monophyly of extant clades is critically important. This study serves to illustrate that there are potential issues with the monophyly of some clades in Emydidae. Critically, as researchers move farther back in time the number of characters available for evaluation will be reduced. If with a reduced number of characters, and a large taxonomic sampling of extant specimens, with minimal missing data, cannot reliably recover extant clades this means by extension that those clades cannot be diagnosed by characters in those datasets. The further extension of this is that when evaluating fossils that may be closely related to extant crown clade taxa, researchers may lack appropriate morphological diagnoses. The

end result is limited confidence in the relationships of extinct fossil organisms and a reduced ability to determine the phylogenetic history of the group. To combat this, studies similar to this one may identify problematic clades (e.g., Deirochelyinae) that may warrant more careful study and evaluation for new and distinct traits that are applicable even when focusing on distinct anatomical regions. An additional potential solution would be to seek out new additional characters, such as those of the long bones or disarticulated cranial elements (Bell and Mead in press, Burroughs Chapter 1 this thesis). In short, if researchers wish to focus on the paleontological record, a careful consideration of extant taxa is critical.

Researchers can use the framework outlined in this study to investigate their own datasets. It is important that they do so, so that robust analyses of extant groups are in place to allow for the use of phylogeny and apomorphy-based identifications of both fossil and extant taxa. In the case of emydid turtles, the use of head or shell data separate of one another does not provide an equal or better estimate of phylogeny. This is something that had been *implicitly assumed* by previous workers, but never carefully evaluated. Instead, these data must be combined, but allowed some degree of independence (such as partitioning in a Bayesian analysis). The conclusion is, thus, that indiscriminate use or preference for one anatomical region over another is not justified in this study.

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Table 2a: List of parsimony analyses with datasets, tree length, and number of clades contained in the analysis.

Analysis	Dataset	Tree Length (Strict Consensus)	Number of Monophyletic Clades
A	245 Morphological Character (Comparison Tree)	911 steps	32
B	159 Characters (Head + Shell)	344 steps	15
C	Shell Only	354 steps	17
D	Head only	300 steps	9
E	Head + Shell Combined with additional outgroups and taxonomic equivalents removed	950 steps	11
F	Shell Only with additional outgroups and taxonomic equivalents removed	1008 steps	18
G	Head Only with additional outgroups and taxonomic equivalents removed	999 steps	9

Table 2b: Number of clades shared between analysis and comparison tree. Clade 1 contains Clades 2 and 11; Clade 2 contains *Emys orbicularis*, *Emydoidea blandingii*, and Clade 3. Clade 3 contains *Clemmys guttata* and Clade 4; Clade 4 contains *Actinemys marmorata* and Clade 5; Clade 5 contains *Glyptemys muhlenbergii* and Clade 6; Clade 6 contains *Glyptemys insculpta* and Clade 7; Clade 7 contains *Terrapene nelsoni* and Clade 8; Clade 8 contains *Terrapene coahuila* and Clade 9; Clade 9 contains *Terrapene carolina triunguis* and Clade 10; Clade 10 contains *Terrapene carolina carolina* and *Terrapene ornata*; Clade 11 contains *Deirochelys reticularia* and Clade 12.

Analysis	Number of Monophyletic clades shared with the Comparison Tree	Clade 1	Clade 2	Clade 3	Clade 4	Clade 5	Clade 6	Clade 7	Clade 8	Clade 9	Clade 10	Clade 11
A		X	X	X	X	X	X	X	X	X	X	X
B	11			X	X	X	X	X	X	X	X	
C	2							X				
D	5				X	X	X			X	X	
E	6			X	X	X		X				
F	1							X				
G	5				X					X	X	

Table 2c: Clade 12 contains *Chrysemys picta* and Clade 13; Clade 13 contains Clades 14 and 21; Clade 14 contains *Trachemys scripta elegans* and Clade 15; Clade 15 contains Clades 16 and 19; Clade 16 contains *Trachemys gaigeae* and Clade 17; Clade 17 contains *Pseudemys peninsularis* and Clade 18; Clade 18 contains *Pseudemys nelsoni* and *Pseudemys rubriventris*; Clade 19 contains *Pseudemys concinna* and Clade 20; Clade 20 contains *Pseudemys gorzugi* and *Pseudemys texana*. Clade 21 contains *Trachemys scripta nebulosa*, *Trachemys scripta venusta*, and Clade 22; Clade 22 contains Clade 23 and Clade 33.

Analysis	Clade 12	Clade 13	Clade 14	Clade 15	Clade 16	Clade 17	Clade 18	Clade 19	Clade 20	Clade 21	Clade 22
A	X	X	X	X	X	X	X	X	X	X	X
B						X					
C											
D											
E						X					
F											
G											

Table 2d: Clade 23 contains *Graptemys ouachitensis sabinensis* and *Graptemys versa*; Clade 24 contains *Graptemys oculifera* and Clade 25; Clade 25 contains *Graptemys flavimaculata* and *Graptemys nigrinoda*; Clade 26 contains *Graptemys ouachitensis ouachitensis* and Clade 27; Clade 27 contains *Graptemys pseudogeographica* and Clade 28; Clade 28 contains *Graptemys geographica* and Clade 29; Clade 29 contains *Graptemys caglei* and Clade 30.
Table 1f: Clade 30 contains *Graptemys barbouri* and Clade 31; Clade 31 contains *Graptemys gibbonsi* and *Graptemys pulchra*; Clade 32 contains *Malaclemys terrapin littoralis* and *Malaclemys terrapin terrapin*; Clade 33 contains Clades 24 and 26.

Analysis	Clade 23	Clade 24	Clade 25	Clade 26	Clade 27	Clade 28	Clade 29	Clade 30	Clade 31	Clade 32	Clade 33
A	X	X	X	X	X	X	X	X	X	X	
B									X	X	
C		X									
D								X	X		
E									X	X	
F											
G								X	X		

Table 3a: List of Bayesian analyses with datasets and parameters compared. Details of among-partition rate prior.

Analysis	Dataset	Number of Partitions	Among-partition rate variation model
A	245 Character (Comparison Tree)	1	N/A
B	Head Only, no additional outgroups	1	N/A
C	Shell Only, no additional outgroups	1	N/A
D	Head Only, additional outgroups	1	N/A
E	Shell Only, additional outgroups	1	N/A
F	Head Only, additional outgroups, outgroup constraint	1	N/A
G	Shell Only, additional outgroups, outgroup constraint	1	N/A
H	159 Character, no additional outgroups	1	N/A
I	159 Character, no additional outgroups	2	Linked Rate Multiplier
J	159 Character, no additional outgroups	2	Unlinked Branch Lengths
K	159 Character, no additional outgroups	2	Unlinked Toopology
L	159 Character, no additional outgroups	2	Unlinked Branch Lengths and Unlinked Topology
M	159 Characters, additional outgroups	1	N/A
N	159 Characters, additional outgroups	2	Linked Rate Multipler
O	159 Characters, additional outgroups	2	Unlinked Branch Lengths
P	159 Characters, additional outgroups	2	Unlinked Topology
Q	159 Characters, additional outgroups	2	Unlinked Branch Lengths and Unlinked Topology
R	159 Characters, additional outgroups, outgroup constraint	1	N/A
S	159 Characters, additional outgroups, outgroup constraint	2	Linked Rate Multipler
T	159 Characters, additional outgroups, outgroup constraint	2	Unlinked Branch Lengths
U	159 Characters, additional outgroups, outgroup constraint	2	Unlinked Topology
V	159 Characters, additional outgroups, outgroup constraint	2	Unlinked Branch Lengths and Unlinked Topology

Table 3b (Contained on next page): Analyses A-V. Estimated model likelihoods and Bayes factors. Three comparisons were made based on dataset type. Preferred model is denoted with an *. Number of clades designates the number of monophyletic clades contained in the tree, excluding the clade including the entire ingroup. Number of monophyletic clades shared with comparison tree. Clade 1 contains *Deirochelys reticularia* and all of Clade 2; Clade 2 contains *Chrysemys picta* and all of Clade 3; Clade 3 contains *Trachemys scripta elegans* and all of Clades 4 and 9; Clade 4 contains Clades 5 and 7; Clade 5 contains *Pseudemys peninsularis* and Clade 6; Clade 6 contains *Pseudemys nelsoni* and *Pseudemys rubriventris*; Clade 7 contains *Pseudemys concinna* and Clade 8; Clade 8 contains *Pseudemys gorzugi* and *Pseudemys nelsoni*.

Analysis	Model Liklelihood (Estimated from Stepping-stone)	Bayes Factor	Number of Clades	Number of Clades Shared with Comparison Tree	Clade 1	Clade 2	Clade 3	Clade 4	Clade 5	Clade 6	Clade 7	Clade 8
A	N/A	N/A	29	N/A								
B	N/A	N/A	12	6						X		
C	N/A	N/A		4								
D	N/A	N/A	9	4						X		
E	N/A	N/A	10	3								
F	N/A	N/A	14	5						X		
G	N/A	N/A	11	5								
H	-2617.57	36.56	22	12				X	X	X		X
I	-2613.34	45.02*	18	13				X	X	X		X
J	-2635.49	0.72	20	14					X	X		X
K	-2635.85	N/A	30	14					X	X		X
L	-2635.00	1.70	11	5						X		
M	-2758.46	47.02	17	14	X			X	X	X		X
N	-2753.07	57.80	14	13					X	X		X
O	-2751.73	60.48	18	14					X	X		X
P	-2709.16	145.62*	9	4						X		
Q	-2781.97	N/A	16	9					X	X		
R	-3000.25	N/A	15	11					X	X		
S	-2748.11	504.28	15	11					X	X		
T	-2747.20	506.10*	22	16	X				X	X		X
U	-2780.09	440.32	11	6						X		
V	-2777.92	444.66	17	10	X				X	X		

Table 3c (Contained on Next Page): Analyses A-V. Clade 9 contains *Trachemys gaigae* and Clades 10 and 11. Clade 10 contains *Trachemys scripta nebulosa* and *Trachemys scripta venusta*; Clade 11 contains *Graptemys versa*, *Graptemys*

ouachitensis sabin, and Clades 12 and 13; Clade 12 contains *Malaclemys terrapin littoralis* and *Malaclemys terrapin terrapin*; Clade 13 contains *Graptemys pseudogeographica* and Clades 14 and 17; Clade 14 contains *Graptemys ouachitensis ouachitensis* and Clade 15; Clade 15 contains *Graptemys flavimaculata* and Clade 16; Clade 16 contains *Graptemys nigrinoda* and *Graptemys oculifera*; Clade 17 contains *Graptemys geographica* and Clade 18; Clade 18 contains Clades 19 and 20; Clade 19 contains *Graptemys gibbonsi and Graptemys pulchra*; Clade 20 contains *Graptemys barbouri* and *Graptemys caglei*; Clade 21 contains *Emys orbicularis*, *Emydoidea blandingii*, and Clade 22; Clade 22 contains *Clemmys guttata* and Clade 23.

Analysis	Clade 9	Clade 10	Clade 11	Clade 12	Clade 13	Clade 14	Clade 15	Clade 16	Clade 17	Clade 18	Clade 19	Clade 20	Clade 21	Clade 22
A														
B		X						X			X		X	
C				X			X	X						
D								X			X			
E				X			X	X						
F				X			X	X						
G				X				X			X		X	
H							X	X					X	X
I							X	X			X		X	X
J							X	X			X		X	X
K							X	X			X		X	X
L								X			X		X	
M							X	X			X		X	X
N							X	X			X		X	X
O							X	X			X		X	X
P								X			X			
Q							X	X			X		X	
R							X	X			X		X	X
S							X	X			X		X	X
T				X			X	X			X		X	X
U				X				X			X		X	
V				X			X	X			X		X	

Table 3d (Contained on next page): Analyses A-V. Clade 23 contains *Actinemys marmorata* and Clade 24.
Table 2g: Clade 24 contains *Glyptemys muhlenbergii* and Clade 25; Clade 25 contains *Glyptemys insculpta* and Clade 26; Clade 26 contains *Terrapene coahuila* and Clade 27; Clade 27 contains *Terrapene carolina triunguis* and Clade 28; Clade 28 contains *Terrapene carolina carolina* and Clade 29; Clade 29 contains *Terrapene nelsoni* and *Terrapene ornata*.

Table 3d:

Analysis	Clade 23	Clade 24	Clade 25	Clade 26	Clade 27	Clade 28	Clade 29
A							
B		X					
C				X			
D		X					
E				X			
F				X			
G		X					
H	X	X	X	X			
I	X	X	X	X			
J	X	X	X	X	X	X	
K	X	X	X	X	X	X	
L		X					
M	X	X		X			
N	X	X	X	X			
O	X	X	X	X	X	X	
P		X					
Q		X		X			
R	X	X	X	X			
S	X	X	X	X			
T	X	X	X	X	X	X	
U		X					
V		X		X			

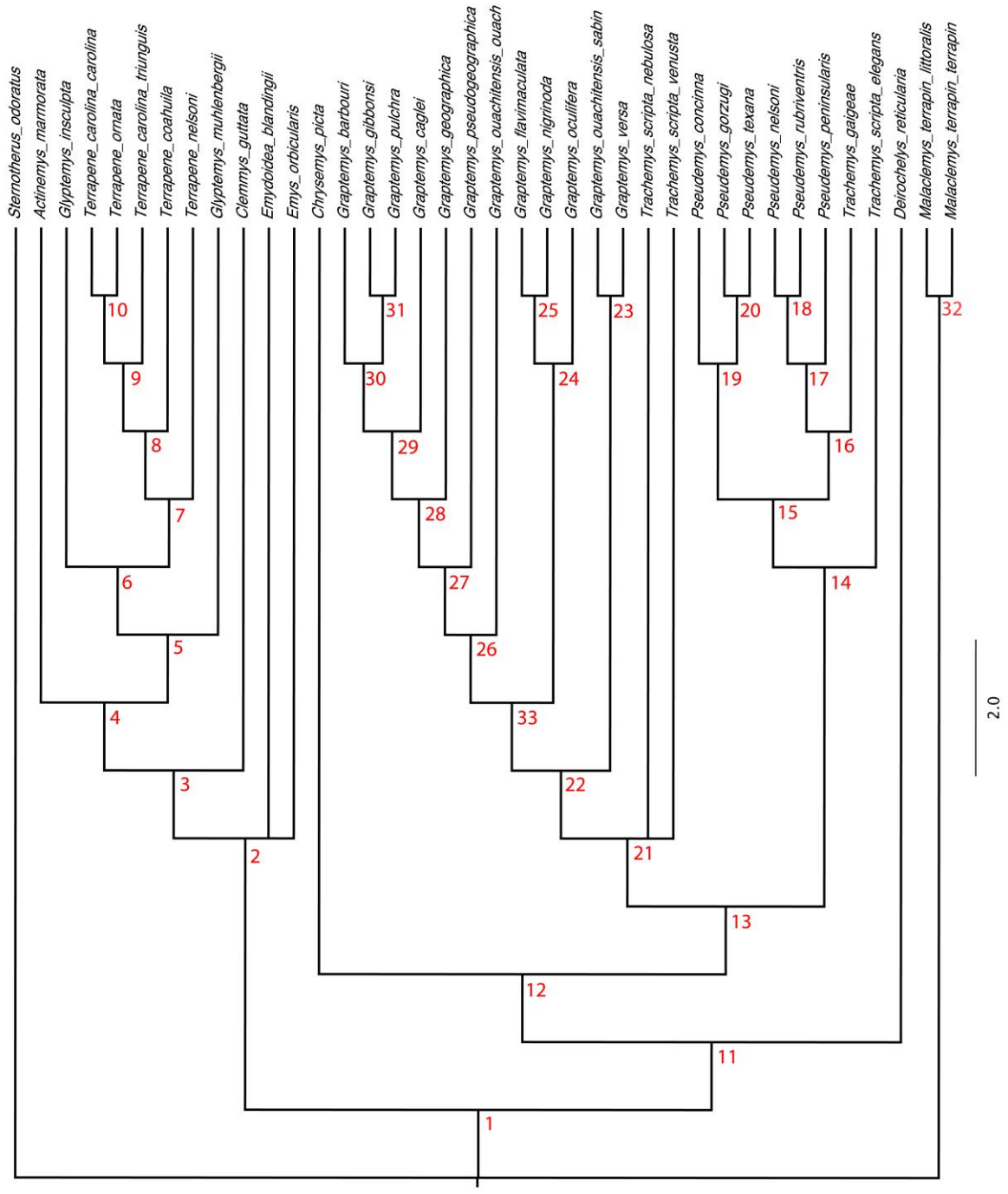

Figure 60: Strict consensus of parsimony comparison tree, 911 steps long, red numbers are arbitrarily assigned clade numbers

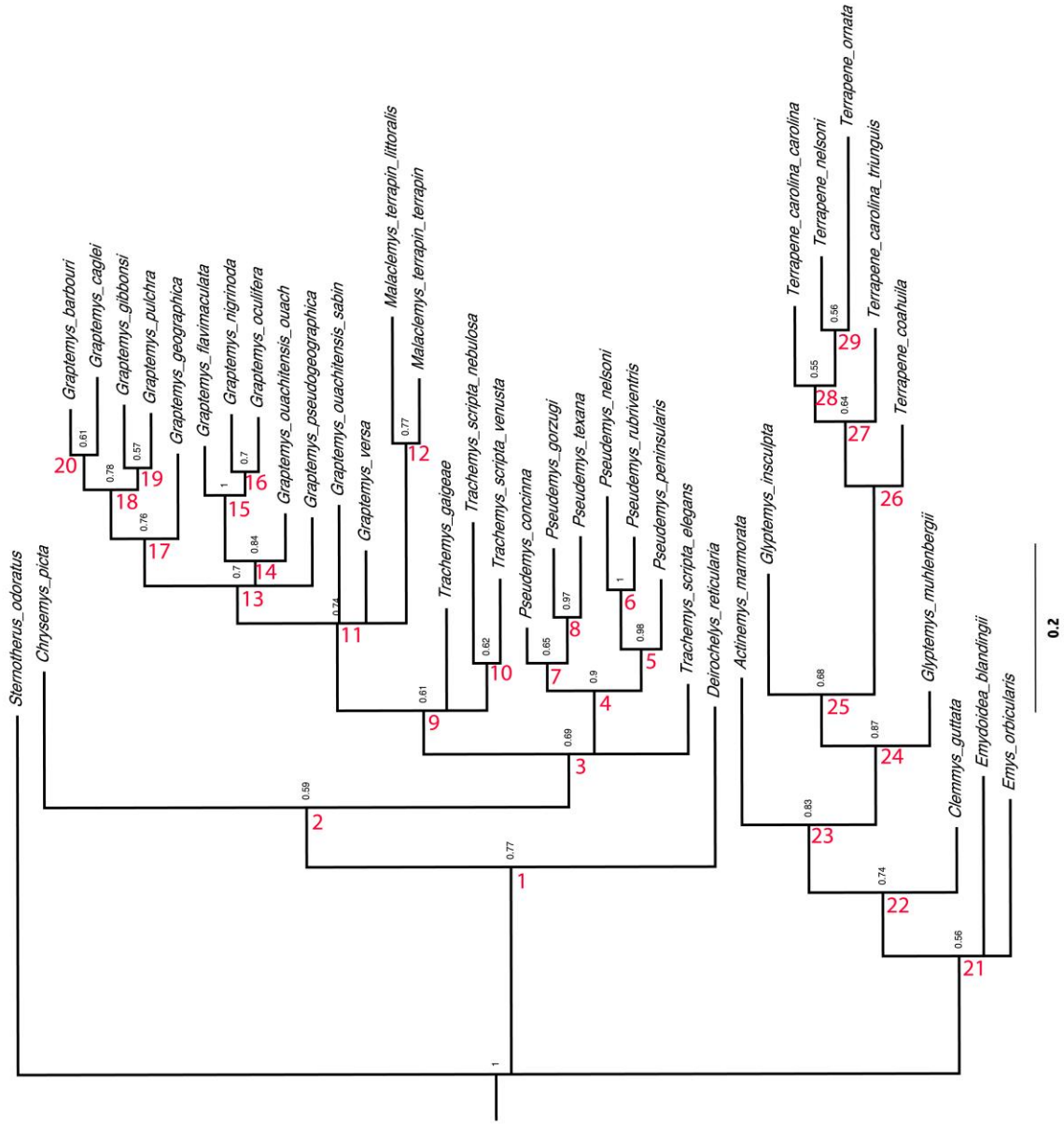

Figure 61: Bayesian consensus tree of Bayesian comparison tree, red numbers are arbitrarily assigned clade numbers, black numbers are Bayesian posterior probabilities.

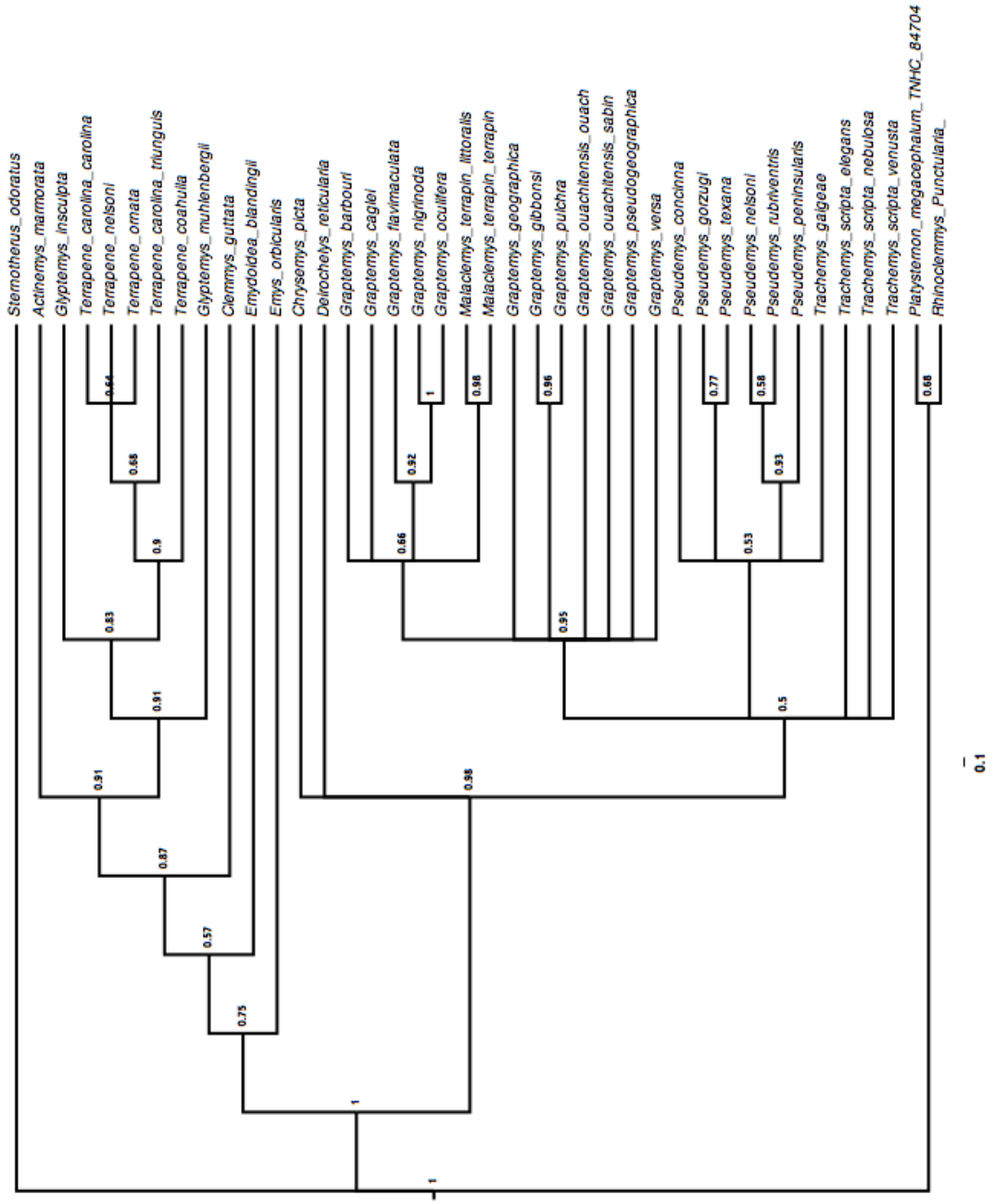

Figure 62: Bayesian consensus tree of Bayesian analysis with 159-characters, in two anatomical partitions, with additional outgroups, with an outgroup constraint, with branch lengths unlinked. Black numbers are posterior probabilities.

Appendices

APPENDIX 1: LIST OF SPECIMENS EVALUATED FOR MORPHOLOGICAL CHARACTERS

Institutional Abbreviations: California Academy of Sciences – CAS; Carnegie Museum of Natural History – CMNH; Senckenberg Natural History Collections Dresden – D; Sam Noble Museum of Natural History – OMNH; Texas Memorial Museum – TMM M; Texas Natural History Collections – TNHC; University of Nebraska State Museum – UNSM; University of Texas –El Paso – UTEP; Peabody Museum of Natural History – YPM R.

Specimens are listed in alphabetical order.

Actinemys marmorata: TNHC 64824
Agrionemys horsfieldii: CAS 228398, CAS 228425
Annamemys annamensis: D-40829
Chelydra serpentina: CAS 228457
Chinemys reevesi: TNHC 69388, TNHC 64814, TNHC 64815
Chrysemys picta: TNHC 69404, CAS 228385
Cuora amboinensis: CAS 228345
Cuora aurocapitata: D-45154
Cuora flavomarginata: CMNH 87474, CMNH 113086
Cuora galbinifrons: D-41868, D-40490
Cuora mccordi: D-45162
Cuora pani: D-41891
Cuora zhoui: D-45163, D-46579
Cyclemys atripons: D-42549, D-42548
Cyclemys dentata: CAS 228333
Cyclemys oldhammi: D-40300, D- 40390
Cyclemys *tcheponensis*: D-44278, CAS 228363
Deirochelys reticularia: OMNH 37928,OMNH 39963, YPM R 16033, YPM R 16033, YPM R 13288, CAS 228388
Dipsochelys dussumieri: OMNH 39849
Emydoidea blandingii: TNHC 85792, TNHC 85793, CAS 228373, CAS 228346, CAS 228448
Emys orbicularis: TNHC 64831, TNHC 64832, D-42967, CAS 228347
Emys trinacris: D-46664
Geochelone nigra: OMNH 39860, OMNH 40579
Geochelone pardalis: OMNH 39853
Geochelone sulcata: YPM R 11445
Geoemyda spengleri: CAS 228343
Glyptemys insculpta: OMNH 39962
Graptemys geographica: OMNH 39965
Graptemys kohni: TNHC 64860, TNHC 64818

Graptemys nigrinoda: CMNH 67407
Graptemys pseudogeographica: OMNH 39966
Gopherus agassizii: OMNH 43874, OMNH 40073, OMNH 40072
Gopherus berlandieri: TNHC 64786, TNHC 62559
Gopherus polyphemus: OMNH 39859, OMNH 40581
Heosemys spinosa: YPM R 12608, YPM R 13984
Indotestudo elongata: CMNH 112249, CMNH 125914
Malaclemys terrapin: TNHC 64834, TNHC 63070, TNHC 66501, CAS 228387, CAS 228340
Malayemys subtrijuga: D-42514, D-42522, CAS 228445, CAS 228446
Manouria impressa: OMNH 43875
Mauremys leprosa: D-4762, D-43362
Mauremys iversoni: D-40653
Melanochelys trijuga: D-38993
Morenia petersi: D-28068
Notochelys platynota: D-41948, CAS 228450
Ocadia sinensis: D-40539, CMNH 118519, CMNH 118511, CMNH 66395, CAS 228339
Platysternon megacephalum: D-40794, TMM M-9672
Pseudemys catespilla: OMNH 34859
Pseudemys texana: CAS 228438, TMM M-8284, TMM M-9960, TMM M-9966, TMM M-12100
Pyxidea mouhotii: CAS 228365, CAS 228444, CAS 228374
Rhinoclemmys funerea: YPM R 14340, YPM R 12174
Rhinoclemmys pulcherimma: CAS 228355, CAS 228377
Rhinoclemmys punctularia: CMNH 124271, CMNH 118581, CMNH 124272, CMNH 118583
Siebenrockiella crassicollis: CAS 228335
Terrapene carolina: CAS 228375, TMM M-12135, TMM M-12134, TMM M-9876, TMM M-9874
Terrapene coahuila: TNHC 68950, TNHC 68360, TNHC 68962, TNHC 68955
Terrapene corneri: UNSM 21618
Terrapene nelsoni: UTEP 1229
Terrapene ornata: TMM M-9878, TMM M-9877, TMM M-9882, TMM M-9880
Terrapene parornata: OMNH 58168
Testudo denticulata: OMNH 39852, OMNH 40071
Testudo graeca: OMNH 40080, YPM R 11852, YPM R 13284, YPM R 10594, YPM R 10599, CAS 228435
Testudo kleinmanni: CAS 228422, CAS 228426, CAS 228431
Trachemys scripta: OMNH 38254, CAS 228436
New Taxon: TMM 40688-93

APPENDIX 2: GENBANK ACCESSION NUMBERS

Rag1:

gi386783987gbJQ5964471
gi197216192gbEU9307881
gi197216234gbEU9308091
gi225195134gbFJ7707421
gi225195136gbFJ7707431
gi225195132gbFJ7707411
gi197216240gbEU9308121
gi225195142gbFJ7707461
gi225195148gbFJ7707491
gi225195138gbFJ7707441
gi225195140gbFJ7707451
gi169639373gbEU0302411
gi169639389gbEU0302491
gi386783981gbJQ5964441
gi386783983gbJQ5964451
gi386783997gbJQ5964521
gi386783999gbJQ5964531
gi386784045gbJQ5964761
gi386784043gbJQ5964751
gi386784041gbJQ5964741
gi386784037gbJQ5964721
gi386784033gbJQ5964701
gi386784029gbJQ5964681
gi353333293gbHQ4423981
gi353333285gbHQ4423941
gi197216224gbEU9308041
gi197216232gbEU9308081
gi197216228gbEU9308061
gi197216230gbEU9308071
gi197216226gbEU9308051
gi225195086gbFJ7707181
gi225195088gbFJ7707191
gi225195094gbFJ7707221
gi225195096gbFJ7707231
gi312597779gbHQ2666601
gi264681990gbGU0856811
gi56682694gbAY6879131
gi197216210gbEU9307971
gi197216200gbEU9307921

gi353333311gbHQ4424071
gi197216194gbEU9307891
gi399144235gbJN6548511
gi56682682gbAY6879061
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gi215398056gbFJ2308581
gi345654783gbHQ2606561
gi365177412embHE5905261
gi365177410embHE5905251
gi386783971gbJQ5964391
gi353333277gbHQ4423901
gi225195090gbFJ7707201
gi225195092gbFJ7707211
gi379054483gbJN9939801
gi379054481gbJN9939791
gi225195118gbFJ7707341
gi225195116gbFJ7707331
gi365177420embHE5905301
gi225195120gbFJ7707351
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gi353333301gbHQ4424021
gi56682696gbAY6879141
gi197216206gbEU9307951
gi56682692gbAY6879121
gi169639365gbEU0302371
gi56682680gbAY6879051
gi379054475gbJN9939761
gi379054473gbJN9939751
gi225195110gbFJ7707301
gi225195112gbFJ7707311
gi225195098gbFJ7707241
gi225195100gbFJ7707251
gi197216188gbEU9307861
gi264681982gbGU0856771
gi213494419gbFJ2308641
gi213494387gbFJ0090251
gi213494389gbFJ0090321

Rag2:

gi98418425gbDQ4973741
gi98418459gbDQ4973911
gi98418461gbDQ4973921

gi98418449gbDQ4973861
gi169639407gbEU0302581
gi169639419gbEU0302641
gi345654773gbHQ2606511
gi98418457gbDQ4973901
gi98418415gbDQ4973691
gi98418411gbDQ4973671
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gi192805738embAM9316091
gi192805734embAM9316071
gi192805750embAM9316151
gi192805754embAM9316171
gi98418403gbDQ4973631
gi365177472embHE5905561
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gi98418429gbDQ4973761
gi98418435gbDQ4973791
gi98418419gbDQ4973711
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gi169639399gbEU0302541
gi365177514embHE5905781
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gi345654779gbHQ2606541
gi98418463gbDQ4973931
gi365177514embHE5905781
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gi345654779gbHQ2606541
gi215398026gbFJ0090261
gi215398028gbFJ0090331
gi215398057gbFJ2308651

ND4:

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gi62719531gbAY9050991
gi284177165gbGQ8959021
gi50881887gbAY6735661
gi50881819gbAY6735321
gi50881711gbAY6734781
gi50881709gbAY6734771

gi50881855gbAY6735501
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gi50881787gbAY6735161
gi50881889gbAY6735671
gi50881755gbAY6735001
gi50881757gbAY6735011
gi50881935gbAY6735901
gi50881937gbAY6735911
gi50881713gbAY6734791
gi50881719gbAY6734821
gi50881715gbAY6734801
gi50881717gbAY6734811
gi284177159gbGQ8958991
gi32493258gbAF3482862
gi62719481gbAY9050741
gi166987148gbEU2775931
gi166987144gbEU2775911
gi166987140gbEU2775891
gi62719483gbAY9050751
gi284177163gbGQ8959011
gi50881775gbAY6735101
gi50881773gbAY6735091
gi50881671gbAY6734571
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gi117557008gbDQ9023291
gi117557004gbDQ9023271
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gi50881663gbAY6734531
gi406668737gbJX3941711
gi50881865gbAY6735551
gi50881695gbAY6734691
gi50881691gbAY6734671
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gi50881689gbAY6734661
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gi50881823gbAY6735341
gi50881677gbAY6734601
gi50881673gbAY6734581
gi401709561embFR8748411
gi401709565embFR8748431
gi406668743gbJX3941741
gi17483807gbAF3482811
gi217330941gbEU9093761
gi109657805gbDQ6464191
gi365177067embHE5903701
gi109657807gbDQ6464201
gi284177161gbGQ8959001
gi109657813gbDQ6464231
gi297185718gbHM0409361
gi50881725gbAY6734851
gi50881721gbAY6734831
gi50881723gbAY6734841
gi50881723gbAY6734841
gi37963303gbAY2596071
gi50881873gbAY6735591

APPENDIX 3: LIST OF MORPHOLOGICAL CHARACTERS EVALUATED

1) Carapace-plastral connection: (0) ligamentous; (1) bony. Burke et al. . 1996 (14); Stephens and Wiens 2003 (81).

2) Plastral Buttresses: (0) absent; (1) present with axillary buttress; (2) present with inguinal buttress; (3) present with both axillary and inguinal buttresses present. Burke et al. . 1996 (17); Minx 1996 (IB); Stephens and Wiens 2003 (82).

3) Thickened peripherals: (0) not thickened; (1) with lateral edges swollen to form lip. Minx 1996 (TP); Stephens and Wiens 2003 (83).

4) Number of neurals: (0) nine or more; (1) eight; (2) seven; (3) six or less. Burroughs et al. (6).

5) Neural one: (0) square 4 sides; (1) pentagonal 5 sides; (2) hexagonal 6 sides; (3) heptagonal 7 sides; (4) octagonal 8 sides. Minx 1996 (NC), Joyce and Bell 2004 (37 and 38) Burroughs et al. (9).

6) Neural two: (0) square 4 sides; (1) pentagonal 5 sides; (2) hexagonal 6 sides; (3) heptagonal 7 sides; (4) octagonal 8 sides. Minx 1996 (NC), Joyce and Bell 2004 (37 and 38) Burroughs et al. (9).

7) Neural three: (0) square 4 sides; (1) pentagonal 5 sides; (2) hexagonal 6 sides; (3) heptagonal 7 sides; (4) octagonal 8 sides. Minx 1996 (NC), Joyce and Bell 2004 (37 and 38) Burroughs et al. (9).

8) Neural four: (0) square 4 sides; (1) pentagonal 5 sides; (2) hexagonal 6 sides; (3) heptagonal 7 sides; (4) octagonal 8 sides. Minx 1996 (NC), Joyce and Bell 2004 (37 and 38) Burroughs et al. (9).

9) Neural five: (0) square 4 sides; (1) pentagonal 5 sides; (2) hexagonal 6 sides; (3) heptagonal 7 sides; (4) octagonal 8 sides. Minx 1996 (NC), Joyce and Bell 2004 (37 and 38) Burroughs et al. (9).

10) Neural six: (0) square 4 sides; (1) pentagonal 5 sides; (2) hexagonal 6 sides; (3) heptagonal 7 sides; (4) octagonal 8 sides. Minx 1996 (NC), Joyce and Bell 2004 (37 and 38) Burroughs et al. (9).

11) Neural seven: (0) square 4 sides; (1) pentagonal 5 sides; (2) hexagonal 6 sides; (3) heptagonal 7 sides; (4) octagonal 8 sides Minx 1996 (NC), Joyce and Bell 2004 (37 and 38) Burroughs et al. (9).

12) Neural eight: (0) square 4 sides; (1) pentagonal 5 sides; (2) hexagonal 6 sides; (3) heptagonal 7 sides; (4) octagonal 8 sides. Minx 1996 (NC), Joyce and Bell 2004 (37 and 38) Burroughs et al. (9).

13) Neural nine: (0) square 4 sides; (1) pentagonal 5 sides; (2) hexagonal 6 sides; (3) heptagonal 7 sides; (4) octagonal 8 sides. Minx 1996 (NC), Joyce and Bell 2004 (37 and 38) Burroughs et al. (9).

14) Inward depression in the posterior half of the fourth costal: (0) absent; (1) present. Minx 1996 (PB); Stephens and Wiens 2003 (94).

15) Number of sides of posterior suprapygal: (0) three; (1) four; (2) five; (3) six; (4) seven or more. Minx 1996 (SP); Stephens and Wiens 2003 (95)Period

16) Suprapygals: (0) separated from neurals by last pair of costals; (1) contacting neurals Stephens and Wiens 2003 (96).

17) Number of suprapygals: (0) none; (1) one; (2) two or more. Stephens and Wiens 2003 (97).

18) Anteri epiplastral margin underlying gular scutes: (0) not swollen; (1) swollen to form lip. Seidel 1994; Stephens and Wiens 2003 (98).

19) Epiplastra: (0) smooth lateral margins; (1) each bearing a toothlike swelling on dorsal surface at margin of gular and humeral scutes. From Stephens and Wiens 2003 (99)

20) Anterior epiplastral margin in ventral view: (0) straight; (1) curved anteromedially and usually forming smooth line with rest of epiplastral margin; (2) curved and bearing shallow medial cleft having an appearance similar to the top of a heart symbol; (3) curved anteriorily, not a smooth curve but does not bear the cleft found in state 2. Seidel 1994; Stephens and Wiens 2003 (100).

21) Anterior epiplastral margin underlying gular scutes in anterior view: (0) straight and flat; (1) curved dorsally at margins; (2) curved ventrally at lateral margins. From Stephens and Wiens 2003 (101).

22) Entoplastron: (0) absent; (1) present. From Stephens and Wiens 2003 (102).

23) Number of sides of entoplastron in ventral view: (0) two; (1) three; (2) four or more. Seidel and Miranda 1984; Stephens and Wiens 2003 (103).

24) Entoplastron: (0) extended anteriorly with majority of element anterior to point of greatest width; (1) anterior and posterior halves of entoplastron equal; (2) entoplastron extended posteriorly with majority of element posterior to point of greatest width. From Stephens and Wiens 2003 (104).

25) Suprascapula: (0) Absent; (1) present. From White 1929; Burke et al. . 1996 (11); Stephens and Wiens 2003 (115).

26) Episcapula: (0) Absent; (1) Present. From White 1929; Burke et al. . 1996 (12); Stephens and Wiens 2003 (116).

27) Cervical vertebrae: (0) not elongate; (1) elongate. From McDowell 1964; Stephens and Wiens 2003 (117).

28) Thoracic rib heads: (0) straight, relatively short and thick; (1) long, slender, and bowed ventrally; (2) long and slender but not bowed ventrally. From McDowell 1964; Stephens and Wiens 2003 (120).

29) Epipubes: White 1929 noted various epipubes shapes and lengths without noting ossification; see page 146 of White: (0) not ossified, cartilaginous; (1) at least partially ossified. From Gaffney and Meylan 1988 (F5.5); Stephens and Wiens 2003 (121).

30) Opening in pelvis: (0) single; (1) two openings present with the anterior and posterior halves of the pelvis contacting medially. From White 1929; Stephens and Wiens 2003 (122).

31) Seams between right and left halves of pelvis: (0) visible; (1) right and left half of pelvis completely fused with seams no longer visible ventrally. From White 1929; Stephens and Wiens 2003 (123).

32) Overall shape of carapace in dorsal external view: (0) circular; (1) oval, sometimes expanded posteriorly with slightly concave lateral edges. From Minx 1996 (EC); Stephens and Wiens 2003 (156).

33) Carapace shape in lateral view: (0) domed having distinct highest point (1) flattened with no distinct highest point. From Milstead 1969; Seidel and Miranda 1984; Stephens and Wiens 2003 (157).

34) Location of highest point of carapace when present: (0) anterior to the midline; (1) at midline; (2) posterior to midline. From Milstead 1969; Stephens and Wiens 2003 (158).

35) Growth annuli of scutes of carapace: (0) distinct; (1) not visible. From Minx 1996 (AN); Stephens and Wiens 2003 (159).

36) Growth point of scutes of carapace (centre of growth annuli): (0) in the middle of each scute; (1) along posterior margin of each scute. From Stephens and Wiens 2003 (160).

37) Pleural scutes: (0) thick, each with a raised point; (1) thin, lacking raised points. From Stephens and Wiens 2003 (161).

38) Longitudinal ridges: (0) present on scutes of carapace; (1) scutes smooth, not bearing ridges apart from growth rings. From Burke et al. . 1996 (7); Stephens and Wiens 2003 (162).

39) Outline of neurals: (0) not visible; (1) visible through dorsal scutes of carapace. From Stephens and Wiens 2003 (163).

40) Anterior marginals of carapace: (0) not serrate; (1) serrate. From Stephens and Wiens 2003 (164).

41) Borders between all marginals posterior to contact of the bridge connection between carapace and plastron: (0) smooth; (1) some or all notched. From Stephens and Wiens 2003 (165).

42) Number of most posterior marginal bearing a notched posterior border among marginals anterior tobridge: (0) Marginal 3; (1) Marginal 4; (2) another marginal besides 3 or 4. From Stephens and Wiens 2003 (167). In specimens where the border between all marginals anterior to the bridge was smooth, this character was scored as unknown (Stephens and Wiens 2003)

43) Posterior marginals median notch: (0) absent; (1) present. From Stephens and Wiens 2003 (168); Median notches generally occur in addition to notches at the borders of posterior marginals (Stephens and Wiens 2003)

44) Markings on dorsal surface of marginals: (0) absent, and marginals monotone; (1) some marking spots, blotches, or lines found on marginals. From Stephens and Wiens 2003 (169).

45) Markings on dorsal surface of marginals, if present, consist of: (0) single dark spot; (1) at posterolateral margin of each marginal, dorsally facing C-shaped markings. From Stephens and Wiens 2003 (170).

46) Pleural scutes: (0) bearing no distinct markings; (1) marked. From Stephens and Wiens 2003 (171).

47) Markings on second pleural scute: (0) absent; (1) multiple spots or speckles only; (2) pattern of curving lines, reticulate pattern, or multiple ocelli (3) large, isolated, ring-shaped mark or large, isolated blotch that does not contact edges of scute; (4) spots or blotches dorsally, vertical lines ventrally, often forming radiating pattern; (5) concentric series of ring-shaped markings; (6) many equally distinct vertically orientated lines, sometimes bifurcated dorsally; (7) one pronounced vertical line sometimes with a few smaller vertical lines, usually bifurcated ventrally and forming an upside-down Y; (8) single light spot. From Seidel and Palmer 1991; Stephens and Wiens 2003 (172).

48) Bright yellow coloration of seams of carapace: (0) absent; (1) present. From Stephens and Wiens 2003 (173).

49) Median keel along dorsal midline of carapace: (0) absent; (1) present. From Burke et al. . 1996 (5); Minx 1996 (MK); Stephens and Wiens 2003 (174); Burroughs et al. 2013 (11).

50) Keel, when present: (0) primarily located on anterior half of carapace; (1) distributed equally on anterior and posterior halves of carapace; (2) primarily located on posterior half of carapace. From Stephens and Wiens 2003 (175).

51) Keel, when present, consists of: (0) single ridge; (1) apically blunt knobs; (2) apically acute serrations. From Stephens and Wiens 2003 (176).

52) Height of keel elements, when present: (0) less than 10% length of scutes on which they occur; (1) more than 17% length of scutes on which they occur. From Stephens and Wiens 2003 (177).

53) Coloration of keel, when keel present: (0) darker than that of surrounding carapace; (1) not distinct; (2) lighter than that of surrounding carapace. From Stephens and Wiens 2003 (178).

54) First vertebral scute: (0) not constricted, edges relatively straight; (1) constricted anteriorly; (2) constricted at midlength forming hourglass shape; (3) constricted posteriorly. From Seidel 1994; Stephens and Wiens 2003 (179).

55) First vertebral: (0) long and narrow, maximum length exceeds maximum width; (1) approximately square width and length roughly equal; (2) short and wide, width exceeds length. From Hirayama 1985 (C); Minx 1996 (MS); Stephens and Wiens 2003 (180); Joyce and Bell 2004 (44); Burroughs et al. 2013 (27)

56) Posteriormost marginals: (0) form smooth, horizontal line with marginals lateral to them; (1) higher than marginals just lateral to them; (2) lower the marginals just lateral to them. From Stephens and Wiens 2003 (181).

57) Orientation of edge of posterior row of marginals: (0) posteroventrally not flared; (1) flared posteriorly or posterodorsally out and up to form a lip. From Stephens and Wiens 2003 (182).

58) Number of plastral hinges: (0) none; (1) one; (2) two. From Stephens and Wiens 2003 (189).

59) Posterior plastron: (0) not closeable; (1) closeable. From Burke et al. . 1996 (15); Stephens and Wiens 2003 (190)

60) Anterior plastron: (0) not closeable; (1) closeable. From Burke et al. 1996 (16); Stephens and Wiens 2003 (191).

61) Seams of plastral bones: (0) not visible; (1) visible through plastral scutes. From Stephens and Wiens 2003 (192).

62) Seams of plastral scutes: (0) not darker than scutes; (1) darker than scutes. From Minx 1996 (DS); Stephens and Wiens 2003 (193).

63) Markings on plastron: (0) absent, scutes of plastron monotone; (1) present. From Stephens and Wiens 2003 (194).

64) Markings on plastron, when present: (0) consist of dark markings on a light background; (1) light markings on a dark background. From Stephens and Wiens 2003 (195).

65) Markings of plastron, when present: (0) located on lateral edges of plastron; (1) in the middle of individual plastral scutes, not contacting edges; (2) along central axis of plastron, spreading along seams of plastron; (3) occur in at least two of the above locations. From Stephens and Wiens 2003 (196).

66) Plastral markings, when present: (0) consist of a single dark figure; (1) isolated markings that are not interconnected. From Seidel and Palmer 1991; Stephens and Wiens 2003 (197).

67) Male plastron: (0) flat; (1) bearing concavity. From Minx 1996 (IL); Stephens and Wiens 2003 (198).

68) Concavity of male plastron, when present: (0) restricted to posterior half of plastron; (1) extends along entire length of plastron. From Stephens and Wiens 2003 (199).

69) Gulars in ventral view: (0) flush with anterior margin of humerals; (1) extend anterior to margin of humerals. From Stephens and Wiens 2003 (200).

70) Humeral-pectoral seam: (0) does not contact, or is posterior to entoplastron; (1) contacts entoplastron. From Hirayama 1985 (X); Crumly 1985; Gaffney & Meylan 1988 (F5.1); Stephens and Wiens 2003 (201); Joyce and Bell 2004 (60); Burroughs et al. 2013 (51).

71) Contour of pectoral-abdominal seam: (0) horizontal; (1) sloped posteromedially to approach abdominal-femoral seam. From Gaffney & Meylan 1988; Stephens and Wiens 2003 (202).

72) Contour of anterior apex of femoral-anal seam: (0) acute; (1) smooth, curving line. From Stephens and Wiens 2003 (203).

73) Notch at lateral edge of femoral-anal seams: (0) absent; (1) present. From Stephens and Wiens 2003 (204).

74) Posteromedial margin of plastron: (0) curved anteromedially; (1) consists of deep V-shaped indentation between posterior annals; (2) forms a horizontal line; (3) rounded posteriorly. From Seidel 1994; Stephens and Wiens 2003 (205).

75) Anterior margin of plastron: (0) not serrate; (1) serrate. From Stephens and Wiens 2003 (206).

76) Posterior margin of plastron: (0) not serrate (1) serrate. From Stephens and Wiens 2003 (207).

77) Inguinal scute: (0) absent; (1) present. From Minx 1996 (IS); Stephens and Wiens 2003 (208); Burroughs et al. 2013 (31).

78) Inguinal scute: (0) with smooth surface, growth rings not visible; (1) with visible growth rings. From Minx 1996 (IS); Stephens and Wiens 2003 (210).

79) Inguinal scute: (0) unmarked; (1) bearing black markings. From Seidel 1994; Stephens and Wiens 2003 (211)

80) Apical scale: (0) absent; (1) present. From Minx 1996 (AS); Stephens and Wiens 2003 (212); Burroughs et al. 2013 (32).

81) Apical scale when present: (0) with visible growth rings; (1) not cornified and with no visible growth rings. From Minx 1996 (AP); Stephens and Wiens 2003 (213); Burroughs et al. 2013 (32).

82) Axillary scute: (0) absent; (1) present. From Minx 1996 (AS); Stephens and Wiens 2003 (214); Burroughs et al. 2013 (25).

83) Bridge of plastron is a dorsal extension of the plastron that is visible externally and contacts the carapace: (0) absent; (1) present. From Stephens and Wiens 2003 (216).

84) Markings on bridge: (0) absent; (1) present consisting of an elongate black blotch or thick black line. From Stephens and Wiens 2003 (217).

85) Dark markings on underside of some or all marginals: (0) absent; (1) present. From Stephens and Wiens 2003 (218).

86) Dark markings under marginals, if present: (0) occur on all marginals; (1) on marginals near bridge only; (2) on all marginals near bridge and anterior to bridge. From Stephens and Wiens 2003 (219).

87) Dark markings under marginals, when present, consist of: (0) irregular blotches; (1) solid dark circles; (2) dark circles with light area inside them or a dark ring; (3) dorsally orientated C-shaped mark; (4) dark spots and irregular reticulate lines; (5) posteriorly orientated C-shaped mark ; (6) light centered circles in the middle of each scute in addition to dark scute borders; (7) single dark lines at the posterior and ventral margin of each scute. From Stephens and Wiens 2003 (220).

88) Snout in lateral view: (0) does not extend anterior to rest of head; (1) extends anterior to rest of head. From Stephens and Wiens 2003 (135).

89) Snout in dorsal view: (0) rounded; (1) roughly squared, with three distinct sides. From Minx 1996 (NG); Stephens and Wiens 2003 (136).

90) Nostrils: (0) round, length and width equal; (1) oval. From Stephens and Wiens 2003 (137).

91) Orientation of nostrils, if oval, in anterior view: (0) horizontal; (1) vertical; (2) diagonal. From Stephens and Wiens 2003 (138).

92) Background colour of head and neck: (0) monotone; (1) two-tone, one color dorsally, another ventrally. From Stephens and Wiens 2003 (139).

93) Markings on head and neck: (0) absent although head may be different colour from neck; (1) present, including stripes, spot,s specks, or blotches present on head and/or neck. From Stephens and Wiens 2003 (140).

94) Markings on head and neck: (0) consist of stripes or curved lines, rarely in combination with specks or spots; (1) spots or speckles with no lines present. From Seidel 1994; Stephens and Wiens 2003 (141).

95) Number of stripes contacting orbit: (0) one stripe; (1) two stripes; (2) three stripes; (3) four or more stripes. Scored as unknown for specimens lacking head and neck stripes. Modified from Seidel and Palmer 1991; Stephens and Wiens 2003 (142).

96) Number of stripes on head: (0) one stripe; (1) two stripes; (2) three stripes; (3) four or more stripes. From Seidel and Palmer 1991; Stephens and Wiens 2003 (143).

97) Light-colored markings resembling hairpins: (0) absent; (1) present on dorsal surface of head. From Stephens and Wiens 2003 (144); this character was scored as unknown for specimens lacking head and neck stripes.

98) Arrow-shaped mark on dorsal surface of snout: (0) absent; (1) present. From Stephens and Wiens 2003 (145).

99) Postorbital mark, a large distinct mark posterior to orbit on lateral surface of head or neck: (0) absent; (1) present. In the case of turtles with prominent head stripes such a mark will be at least twice the thickness of other head and neck stripes and/or of a different color. From Stephens and Wiens 2003 (146).

100) Orientation of postorbital mark if present: (0) horizontal; (1) vertical. From Stephens and Wiens 2003 (147).

101) Postorbital markings if present: (0) does not contact orbit; (1) contacts orbit. From Stephens and Wiens 2003 (149).

102) Postorbital mark: (0) isolated from neck stripes; (1) contacts neck stripes. Scored as unknown in specimens that did not have both neck stripes and at least one postorbital mark. Modified from Stephens and Wiens 2003 (150).

103) Middorsal mark: (0) absent; (1) present. Scored as unknown in specimens that did not have both a middorsal mark and at least one postorbital mark. Modified from Stephens and Wiens 2003 (151).

104) Mid-dorsal mark: (0) does not contact postorbital mark; (1) contacts postorbital mark. From Stephens and Wiens 2003 (152).

105) Mandibular stripe, a large distinct stripe running along lower jaw, distinct from, and at least twice the thickness of other stripes on lower jaw: (0) absent; (1) present. From Stephens and Wiens 2003 (153).

106) Mandibular stripe, when present: (0) not forked; (1) forked anteriorly. From Stephens and Wiens 2003 (154).

107) Mandibular stripe, when present: (0) does not contact one or more neck stripes; (1) contacts one or more neck stripes; Stephens and Wiens 2003 (159).

108) Claws on manus of adult male: (0) digits III and IV will bear elongate claws; (1) all same size as, or only slightly longer than, adjacent claws; (2) elongate, some more than twice as long as some adjacent claws. From Seidel and Miranda 1984; Stephens and Wiens 2003 (221).

109) Claws on manus of males: (0) curved; (1) straight. From Seidel and Miranda 1984; Stephens and Wiens 2003 (222).

110) Digits of male manus bearing elongate claws: (0) II and III; (1) II, III, and IV. From Stephens and Wiens 2003 (223).

111) Number of emergent hind claws: (0) four; (1) three. From Minx 1996; Stephens and Wiens 2003 (224).

112) Hind-foot webbing: (0) absent; (1) extending only to proximal margin of claws; (2) extending nearly to distal end of claws. From Burke et al. 1996; Stephens and Wiens 2003 (225).

113) Clasping claws: (0) absent; (1) present. From Minx 1996; Stephens and Wiens 2003 (226).

114) Scales on the forelimbs: (0) relatively flat; (1) convex, protruding outward and appearing bulbous or rugose. From Minx 1996; Stephens and Wiens 2003 (227).

115) Color of scales on forelimbs: (0) same as that of skin on forelegs; (1) different from colour of skin on forelegs. From Stephens and Wiens 2003 (228).

116) Scales on outer edge of forelimbs: (0) serrate; (1) not serrate. From Stephens and Wiens 2003 (229).

117) Stripes on forelimbs: (0) absent; (1) present. From Stephens and Wiens 2003 (230).

118) Number of stripes on forelimb: (0) one; (1) two; (2) three; (3) four or more. From Stephens and Wiens 2003 (231).

119) Posterior surface of hindlimb: (0) unmarked; (1) marked with stripes or spots. From Stephens and Wiens 2003 (232).

120) Shape of the fissura ethmoidalis: (0) narrow; (1) closed keyhole-shaped. From Crumly 1982 (13); Hirayama 1985 (1); McCord et al. 1995 (5); Joyce and Bell 2004 (1).

121) Medial inflection of the inferior descending processes of the frontal: (0) absent; (1) very small; (2) present, well developed medial contact present or almost present. From Hirayama 1985 (2); Joyce and Bell 2004 (2).

122) Frontal contribution to the orbital rim: (0) present, no prefrontal-postorbital contact on dorsal surface; (1) absent, frontal excluded from orbital rim by prefrontal-postorbital contact. From Crumly 1982 (17); Hirayama 1985 (3); Shaffer et al. 1997 (97); Yasukawa et al. 2001 (1); Joyce and Bell 2004 (3).

123) Contact between jugal and pterygoid: (0) present, medial process of jugal well developed and touching the pterygoid; (1) absent, medial process reduced. From Hirayama 1985 (11) (12); McCord et al. 1995 (3); Burke et al. 1996 (23); Yasukawa et al. 2001 (4) (5); Joyce and Bell 2004 (4).

124) Contact of the inferior process of the parietal with the medial process of the jugal: (0) absent; (1) present. From Hirayama 1985 (13); Joyce and Bell 2004 (7).

125) Contact of the inferior process of the parietal with the maxilla: (0) absent; (1) present. From Hirayama 1985 (14); Joyce and Bell 2004 (8).

126) Extent of quadratojugal: (0) quadratojugal well developed, firmly attached to jugal; (1) quadratojugal present, contact lost with jugal; (2) quadratojugal so heavily reduced that it appears to be absent in many skeletal specimens. From Hirayama 1985 (16); Shaffer et al. 1997 (47); Burke et al. 1996 (21); McCord et al. 1995 (6); Yasukawa et al. 2001 (7) (8); Joyce and Bell 2004 (9).

127) Contribution of jugal to the rim of upper temporal emargination: (0) absent; (1) present. From Hirayama 1985 (15); Joyce and Bell 2004 (10).

128) Contact between the quadratojugal and the articular facet of the quadrate: (0) absent; (1) present, quadratojugal sends a process ventrally along the rim of the cavum tympani and touches the lateral edge of the articular facet. From Hirayama 1985 (17); Joyce and Bell 2004 (11).

129) Contact between quadratojugal and maxilla: (0) absent; (1) present. From Hirayama 1985 (18); Joyce and Bell 2004 (12).

130) Medial contact of the maxillae along the anterior margin of the jaw: (0) absent; (1) present. From Hirayama 1985 (20); McCord et al. 1995 (2); Yasukawa et al. 2001 (10); Joyce and Bell 2004 (13).

131) Size of the foramen orbito nasale: (0) small less than one-sixth of orbit length; (1) large more than one-sixth of orbit length. From Hirayama 1985 (33); Gaffney and Meylan 1988 (F9.3) (F10.2) (G10.3) (H11.1) (H16.3); Crumly 1982 (25); Crumly 1994 (12); Joyce and Bell 2004 (14).

132) Contact between maxilla and vomer: (0) present; (1) absent, vomer separated from the maxilla by the premaxilla. From Hirayama 1985 (31); Crumly 1982 (21); Yasukawa et al. 2001 (14); Joyce and Bell 2004 (15).

133) Size of the foramen palatinum posterius: (0) large; (1) small. From Hirayama 1985 (22); Gaffney and Meylan 1988 (F2.2) (F6.1); McCord et al. 1995 (4); Yasukawa et al. 2001 (12); Joyce and Bell 2004 (16).

134) Position of the pterygoid relative to foramen palatinum posterius (fpp): (0) pterygoid situated posterior to the fpp; (1) pterygoid situated posterior to the fpp but sends a process anterior and lateral to the fpp. From Joyce and Bell 2004 (17).

135) Epipterygoid participation in the trigeminal foramen: (0) absent; (1) present, epipterygoid clearly separates the parietal and pterygoid in lateral view. From Joyce and Bell 2004 (18).

136) Development of the foramen praepalatinum as a canal, canalis praepalatinum, that is concealed by a bony secondary palate in ventral view: (0) absent; (1) present. From Hirayama 1985 (24); Joyce and Bell 2004 (20).

137) Contact between pterygoid and basioccipital: (0) present; (1) absent. From Gaffney and Meylan 1988 (F1.1) (F10.3) (H18.3); Crumly 1994; Shaffer et al. 1997 (103); Joyce and Bell 2004 (21).

138) Contact of the pterygoid with the articular facet of the quadrate: (0) absent; (1) present. From Hirayama 1985 (38); Joyce and Bell 2004 (22).

139) Closure and depth of the incisura columella auris: (0) absent, incisura is open; (1) present, incisura closed. From Crumly 1985; Gaffney and Meylan 1988 (H1.3); Joyce and Bell 2004 (23).

140) Angular contribution to the sulcus cartilaginis Meckelii: (0) present, the angular contributes to the sulcus and is as long as, or longer than, the prearticular; (1) absent, the angular is shorter than the prearticular. From Gaffney and Meylan 1988 (F1.4); Joyce and Bell 2004 (24).

141) Contact between surangular and dentary: (0) simple contact; (1) strongly interdigitated suture. From Crumly 1982 (12); Crumly 1985; Gaffney and Meylan 1988 (H6.1); Joyce and Bell 2004 (25).

142) Height of the processus coronoideus: (0) as high as dentary; (1) rising significantly above the dentary. From Hirayama 1985 (45); Joyce and Bell 2004 (26).

143) Foramen dentofaciale majus: (0) small; (1) large and situated within a large lateral fossa. From Hirayama 1985 (47); Joyce and Bell 2004 (27).

144) Participation of palatine in the triturating surface of the upper jaw: (0) absent; (1) present. From Hirayama 1985 (26); Gaffney and Meylan 1988 (F2.1); Joyce and Bell 2004 (28).

145) Participation of the vomer in the triturating surface of the upper jaw: (0) absent; (1) present. From Hirayama 1985 (25); Joyce and Bell 2004 (29).

146) Presence and number of lingual ridges of the triturating surfaces of the upper and lower jaws: (0) no lingual ridges present; (1) one lingual ridge present; (2) two lingual ridges present. From Hirayama 1985 (29) (44); Gaffney and Meylan 1988 (F7.2) (F9.1); Joyce and Bell 2004 (30).

147) Well developed serrations on labial or lingual ridges of the triturating surfaces of the upper and lower jaws: (0) absent; (1) present. From Hirayama 1985 (21) (27) (41) (43) (46); Gaffney and Meylan 1988 (F9.2); Yasukawa et al. 2001 (11); Joyce and Bell 2004 (31).

148) Median ridge or sulcus of the triturating surface of the upper jaw: (0) both structures absent; (1) median ridge present; (2) median sulcus present. From Hirayama 1985 (30); Crumly 1985 (4); Gaffney and Meylan 1988 (H3.1); Joyce and Bell 2004 (32).

149) Posterior extension of the lower triturating surface behind the symphysis of the dentary: (0) absent; (1) present. From Hirayama 1985 (42); Gaffney and Meylan 1988 (G5.2); Joyce and Bell 2004 (33).

150) Shape of coracoid blade: (0) long and narrow; (1) short and wide; (2) long and wide. From Crumly 1985; Gaffney and Meylan 1988 (H1.7); Joyce and Bell 2004 (66).

151) Webbing between digits: (0) present, well developed; (1) absent, or at least strongly reduced. From Hirayama 1985 (b); Joyce and Bell 2004 (69).

152) Sexual size dimorphism: (0) absent; (1) present, female much larger than male. From Gaffney and Meylan 1988 (F5.2); Burke et al. 1996 (37); Joyce and Bell 2004 (70).

153) Co-ossification of carapacial bones: (0) absent; (1) present in more than 50% of the bones in the carapace. From Minx 1996 (CO); Burroughs et al. 2013 (16).

154) Contact between first vertebral and second marginal scutes: (0) absent; (1) present. From Hirayama 1985 (O); Joyce and Bell 2004 (47); Burroughs et al. 2013 (20).

155) Contact between the third pleural and sixth marginal scutes: (0) absent; (1) present. From Hirayama 1985 (B); Joyce and Bell 2004 (48); Burroughs et al. 2013 (21).

156) Contact between the fifth vertebral and tenth marginal scutes: (0) absent; (1) present; Hirayama 1985 (K); Joyce and Bell 2004 (46); Burroughs et al. 2013 (22).

157) Twelfth marginal scute: (0) two present, with their common sulcus partially dividing the pygal; (1) two present, but their common sulcus fully divides the pygal; (2) twelfth marginal scutes fused along the midline. From Joyce and Bell 2004 (49); Burroughs et al. 2013 (23).

158) Presence of a cervical scute: (0) absent; (1) present. From Joyce and Bell 2004 (40); Burroughs et al. 2013 (24).

159) Position of the anterior sulcus of the fourth vertebral: (0) sulcus lies on fifth neural; (1) sulcus lies on fourth neural or on the suture between the fourth and fifth neurals; (2) sulcus lies on the sixth neural or on the suture between the fifth and sixth neurals. From Hirayama 1985 (L) (M); Joyce and Bell 2004 (42); Burroughs et al. 2013 (29).

160) Position of the posterior sulcus of the fourth vertebral: (0) sulcus lies on the eighth neural or on the homologue of the eighth neural; (1) sulcus lies on the seventh neural or on the suture between the seventh and eighth neurals; (2) eighth neural absent and sulcus overlies costals that meet at midline. From Hirayama 1985 (L) (M); Joyce and Bell 2004 (43); Burroughs et al. 2013 (30).

161) Portion of posterior tip of the gular scute extends onto entoplastron: (0) absent; (1) present. Modified from Burroughs et al. 2013 (38).

162) Contact between opposite gular and humeral scutes: (0) no contact between opposite scutes; (1) contact present. From Burroughs et al. 2013 (39).

163) Contact between opposite humeral and pectoral scutes: (0) no contact between opposite scutes; (1) left humeral scute contacts right pectoral scute; (2) right humeral scute contacts left pectoral scute. From Burroughs et al. 2013 (40).

164) Contact between opposite pectoral and abdominal scutes: (0) no contact between opposite scutes; (1) left pectoral scute contacts right abdominal scute; (2) right pectoral scute contacts left humeral scute. From Burroughs et al. 2013 (41).

165) Contact between opposite abdominal and femoral scutes: (0) No contact between opposite scutes; (1) left abdominal scute contacts right femoral scute; (2) right abdominal scute contacts left femoral scute. From Burroughs et al. 2013 (42).

166) Contact between opposite femoral and anal scutes: (0) No contact between opposite scutes; (1) left femoral scute contacts right anal scute; (2) right femoral scute contacts left anal scute. From Burroughs et al. 2013 (43).

167) Absence or presence of epiplastral beak on the anterior lobe of the plastron: (0) absent; (1) present. Modified from Holman and Fritz 2005; Burroughs et al. 2013.

168) Position of the humeral-pectoral sulcus with respect to the anterior-posterior midline of the entoplastron: (0) approximately at the midline of the entoplastron; (1) sulcus shifted significantly anterior to the midline of the entoplastron; (2) sulcus shifted significantly posterior to the midline of the entoplastron orbital rim. From Crumly 1982 (17); Hirayama 1985 (3); Shaffer et al. 1997 (97); Yasukawa et al. 2001 (1); Holman and Fritz 2005; Burroughs et al. 2013 (50).

169) Concavity on the ventral surface of fused pelvis: (0) absent; (1) present.

170) Depth of concavity on ventral surface of fused pelvis, when present: (0) shallow; (1) deep.

171) Angle between acromion process and scapular process: (0) approximately 90 degrees; (1) less than 90 degrees; (2) greater than 90 degrees.

172) Number of pairs of peripheral bones: (0) 10 pairs; (1) 11 pairs; (2) 12 pairs; (3) Less than 10 pairs; (4) Greater than 12 pairs. From Burroughs et al. 2013 (8).

173) Number of pairs of costal bones: (0) 7 pairs; (1) 8 pairs; (2) less than 7 pairs; (3) greater than 8 pairs. From Burroughs et al. 2013 (7).

174) Number of pairs of marginal scutes: (0) 10{{delete space}}; (1) 11; (2) 12; (3) less than 10; (4) greater than 12. From Burroughs et al. 2013 (19).

175) Number of vertebral scutes: (0) 3; (1) 4; (2) 5; (3) less than 3; (4) greater than 5. From Burroughs et al. 2013 (17).

176) Number of pairs of pleural scutes: (0) 3; (1) 4; (2) 5; (3) less than 3; (4) greater than 5. From Burroughs et al. 2013 (18).

177) Presence of inframarginal scutes: (0) absent; (1) present. From Gaffney and Meylan 1988 (A14.1).

178) Presence of the coalesence of the femoral trochanters on the ventral surface of the femur: (0) absent; (1) present. From Gaffney and Meylan 1988 (H1.9).

179) Presence of costiform processes on the nuchal: (0) absent; (1) present.

APPENDIX 4: NEXUS FILE

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#NEXUS
BEGIN DATA;
	TITLE  Character_Matrix;
	DIMENSIONS NTAX=140 NCHAR=179;
	FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = "  0 1 2 3 4 5 6
7 8 9 A B C D E F G H J K M N P Q R S T U V W X Y Z a b c d e f g h j k m n p q";
	CHARSTATELABELS
		1 Carapace_Plastral_connection_Burke_et_al_1996_Stephens_and_Wiens_2003 /
ligamentous bony, 2 Plastral_Buttresses_Burke_et_al_1996_Minx_1996_Stephens_and_Wiens_2003
/  absent present_with_axillary_buttress_present with_inguinal_buttress_present
with_both_axillary_and_inguinal_buttress_present, 3
Thickened_peripherals_Minx_1996_Stephens_and_Wiens_2003 /  not_thickened
with_lateral_edges_swollen_to_form_lip, 4
Number_of_Neurals_Joyce_and_Bell_2004_Burroughs_et_al_2012 /  Nine_or_more Eight Seven
Six_or_less, 5 Neural_One /  Square_4_sides Pentagonal_5_sides Hexagonal_6_sides
Heptagonal_7_sides Octagonal_8_sides, 6 Neural_Two /  Square_4_sides Pentagonal_5_sides
Hexagonal_6_sides Heptagonal_7_sides Octagonal_8_sides, 7 Neural_Three /  Square_4_sides
Pentagonal_5_sides Hexagonal_6_sides Heptagonal_7_sides Octagonal_8_sides, 8 Neural_Four /
Square_4_sides Pentagonal_5_sides Hexagonal_6_sides Heptagonal_7_sides Octagonal_8_sides, 9
Neural_Five /  Square_4_sides Pentagonal_5_sides Hexagonal_6_sides Heptagonal_7_sides
Octagonal_8_sides, 10 Neural_Six /  Square_4_sides Pentagonal_5_sides Hexagonal_6_sides
Heptagonal_7_sides Octagonal_8_sides, 11 Neural_Seven /  Square_4_sides Pentagonal_5_sides
Hexagonal_6_sides Heptagonal_7_sides Octagonal_8_sides, 12 Neural_Eight /  Square_4_sides
```

Pentagonal_5_sides Hexagonal_6_sides Heptagonal_7_sides Octagonal_8_sides, 13 Neurals_Nine / Square_4_sides Pentagonal_5_sides Hexagonal_6_sides Heptagonal_7_sides Octagonal_8_sides, 14 Inward_depression_in_the_posterior_half_of_the_fourth_costal_Minx_1996_Stephens_and_Wiens_2004 / absent present, 15 Number_of_sides_of_posterior_superpygal_Minx_1996_Stephens_and_Wiens_2004 / Three Four Five Six Seven_or_more, 16 Suprapygals_Stephens_and_Wiens_2004 / separated_from_neurals_by_last_pair_of_costals contacting_neurals, 17 Number_of_suprapygals_Stephens_and_Wiens_2003_Joyce_and_Bell_2004_Burroughs_et_al_2012 / None One Two_or_more_, 18 Anterior_epiplastral_margin_underlying_gular_scutes_Seidel_1994_Stephens_and_Wiens_2003 / not_swollen swollen_to_form_lip, 19 Epiplastra_Stephens_and_Wiens_2003 / smooth_lateral_margins each_bearing_a_toothlike_swelling_on_dorsal_surface_at_margin_of_gular_and_humeral_scutes, 20 Anterior_epiplastral_margin_in_ventral_view_Seidel_1994_Stephens_and_Wiens_2003 / straight curved_anteromedially_and_usually_forming_smooth_line_with_rest_of_epiplastral_margin curved_and_bearing_shallow_medial_cleft_having_an_appearance_similar_to_the_top_of_a_heart_symbol 'Curved anteriorily, not a smooth curve, but does not bear the cleft found in state 2', 21 Anterior_epiplastral_margin_underlying_gular_scutes_in_anterior_view_Stephens_and_Wiens_2003 / straight_and_flat curved_dorsally_at_margins curved_ventrally_at_lateral_margins, 22 Entoplastron_Stephens_and_Wiens_2003_Joyce_and_Bell_2004 / absent present, 23 Number_of_sides_of_entoplastron_in_ventral_view_Seidel_and_Miranda_1984_Stephens_and_Wiens_2003 / Two Three Four_or_more, 24 Entoplastron_Stephens_and_Wiens_2003 / extended_anteriorly_with_majority_of_element_is_anterior_to_point_of_greatest_width anterior_and_posterior_halves_of_entoplastron_equal or_entoplastron_extended_posteriorly_with_majority_of_element_posterior_to_point_of_greatest_width, 25 Suprascapula_White_1929_Burke_et_al_1996_Minx_1996_Stephens_and_Wiens_2003 / Absent present, 26 Episcapula_White_1929_Burke_et_al_1996_Minx_1996_Stephens_and_Wiens_2003 / Absent Present, 27 Cervical_vertebrae_McDowell_1964_Stephens_and_Wiens_2003 / not_elongate elongate, 28 Thoracic_rib_heads_McDowell_1964_Stephens_and_Wiens_2003 / straight_relatively_short_and_thick long_slender_and_bowed_ventrally long_and_slender_but_not_bowed_ventrally, 29 Epipubes_Gaffney_and_Meylan_1988_Stephens_and_Wiens_2003_White_1929_noted_various_epipubes_shapes_and_lengths_without_noting_ossification_see_page_146_of_White's_thesis / not_ossified_cartilaginous at_least_partially_ossified, 30 Opening_in_pelvis_White_1929_Stephens_and_Wiens_2003 / single two_openings_present_with_the_anterior_and_posterior_halves_of_the_pelvis_contacting_medially, 31 Seams_between_right_and_left_halves_of_pelvis_White_1929_Stephens_and_Wiens_2003 / visible right_and_left_half_of_pelvis_completely_fused_with_seams_no_longer_visible_ventrally, 32 Overall_shape_of_carapace_Minx_1996_Stephens_and_Wiens_2003_Burroughs_et_al_in_dorsal_external_view / circular oval_sometimes_expanded_posteriorly slightly_concave_lateral_edges, 33 Carapace_shape_in_lateral_view_Milstead_1969_Seidel_and_Miranda_1984_Minx_1996_Stephens_

and_Wiens_2003_Burroughs_et_al / domed_having_distinct_‘highest_point’ flattened_with_no_distinct_highest_point, 34 Location_of_highest_point_of_carapace_when_present_Milstead_1969_Stephens_and_Wiens_2003_Burroughs_et_al_ / anterior_to_the_midline at_midline posterior_to_midline, 35 Growth_annuli_of_scutes_of_carapace_Minx_1996_Stephens_and_Wiens_2003_Burroughs_et_al_In_Press / distinct not_visible, 36 Growth_point_of_scutes_of_carapace_centre_of_growth_annuli_Stephens_and_Wiens_2003 / in_the_middle_of_each_scute along_posterior_margin_of_each_scute, 37 Pleural_scutes_Stephens_and_Wiens_2003_As_is_standard_in_my_discussion_of_thick_and_thin_these_terms_lack_quantification_and_as_a_result_clear_repeatability_when_dealing_with_the_variation_present_within_a_taxon_or_across_a_tree / thick_each_with_a_raised_point thin_lacking_raised_points, 38 Longitudinal_ridges_Burke_et_al_1996_Stephens_and_Wiens_2003 / present_on_scutes_of_carapace scutes_smooth_not_bearing_ridges_apart_from_growth_rings, 39 Outline_of_neurals_Stephens_and_Wiens_2003_fusion_when_scoring_this_character_No_note_is_mentioned / not_visible visible_through_dorsal_scutes_of_carapace, 40 Anterior_marginals_of_carapace_Stephens_and_Wiens_2003 / not_serrate serrate, 41 Borders_between_all_marginals_posterior_of_contact_of_the_bridge_connection_between_carapace_and_plastron_Stephens_and_Wiens_2003 / smooth some_or_all_notched, 42 Number_of_most_posterior_marginal_bearing_a_notched_posterior_border_among_marginals_anterior_of_bridge_Stephens_and_Wiens_2003_In_specimens_where_the_border_between_all_marginals_anterior_of_the_bridge_was_smooth_this_character_was_scored_as_unknown / Marginal_3 Marginal_4 another_marginal_besides_3_or_4, 43 Posterior_marginals_median_notch_Stephens_and_Wiens_2003_Median_notches_generally_occur_in_addition_to_notches_at_the_borders_of_posterior_marginals / absent or_present, 44 Markings_on_dorsal_surface_of_marginals_Stephens_and_Wiens_2003_ / absent_and_marginals_monotone or_some_marking_spots_blotches_or_lines_found_on_marginals, 45 Markings_on_dorsal_surface_of_marginals_if_present_consist_of_Stephens_and_Wiens_2003_Emydids_display_a_bewildering_diversity_of_marginal_markings_as_a_group_In_order_to_deal_with_this_variation_in_a_conservative_manner_assumptions_about_the_independence_and_homology_of_the_various_types_of_markings_were_minimized_i_e_type_of_marginal_markings_was_treated_as_a_single_unordered_character_and_the_states_of_this_character_were_chosen_such_that_only_specimens_with_very_similar_marginal_markings_would_receive_the_same_score / single_dark_spot_at_posterolateral_margin_of_each_marginal dorsally_facing_C_shaped_markings, 46 Pleural_scutes_Stephens_and_Wiens_2003 / bearing_no_distinct_markings or_marked, 47 Markings_on_second_pleural_scute_Seidel_&_Palmer_1991_Stephens_and_Wiens_2003_As_with_marginals_markings_emydid_display_considerable_diversity_in_pleural_scute_markings_This_variation_was_dealt_with_in_a_similar_manner_by_coding_pleural_scute_markings_as_a_single_unordered_character_with_states_chosen_such_that_only_specimens_with_very_similar_markings_would_receive_the_same_score / absent multiple_spots_or_speckles_only pattern_of_curving_lines_reticulate_pattern_or_multiple_ocelli large_isolated_ring_shaped_mark_or_large_isolated_blotch_that_does_not_contact_edges_of_scute spots_or_blotches_dorsally_vertical_lines_ventrally_often_forming_radiating_pattern

concentric_series_of_ring_shaped_markings
many_equally_distinct_vertically_orientated_lines_sometimes_bifurcated_dorsally
one_pronounced_vertical_line_sometimes_with_a_few_smaller_vertical_lines_usually_bifurcated_v
entrally_and_forming_upsidedown_Y single_light_spot, 48
Bright_yellow_colouration_of_seams_of_carapace_Stephens_and_Wiens_2003 / absent or_present,
49 Median_keel_along_dorsal_midline_of_carapace_Burke_et_al_1996_Stephens_and_Wiens_2003
/ absent present, 50 Keel_when_present_Stephens_and_Wiens_2003 /
primarily_located_on_anterior_half_of_carapace
distributed_equally_on_anterior_and_posterior_halves_of_carapace
or_primarily_located_on_posterior_half_of_carapace, 51
Keel_when_present_consists_of_Stephens_and_Wiens_2003 / single_ridge apically_blunt_knobs
or_apically_acute_serrations, 52
Height_of_keel_elements_when_present_Stephens_and_Wiens_2003 /
less_than_10%_length_of_scutes_on_which_they_occur
or_more_than_17%_length_of_scutes_on_which_they_occur, 53
Coloration_of_keel_when_keel_present_Stephens_and_Wiens_2003 /
darker_than_that_of_surrounding_carapace not_distinct
or_lighter_than_that_of_surrounding_carapace, 54
First_vertebral_scute_Seidel_1994_Stephens_and_Wiens_2003 /
not_constricted_edges_relatively_straight constricted_anteriorly
or_constricted_at_midlength_forming_hourglass_shape constricted_posteriorly, 55
First_vertebral_Minx_1996_Stephens_and_Wiens_2003_Burroughs_et_al /
long_and_narrow_maximum_length_exceeds_maximum_width
square_width_and_length_roughly_equal or_short_and_wide_width_exceeds_length, 56
Posteriormost_marginals_Stephens_and_Wiens_2003 /
form_smooth_horizontal_line_with_marginals_lateral_to_them
or_higher_than_marginals_just_lateral_to_them lower_the_marginals_just_lateral_to_them, 57
Orientation_of_edge_of_posterior_row_of_marginals_Stephens_and_Wiens_2003 /
posteroventral_not_flared or_flared_posteriorly_or_posterodorsally_out_and_up_to_form_lip, 58
Number_of_plastral_hinges_Stephens_and_Wiens_2003 / none one or_two, 59
Posterior_plastron_Burke_et_al_1996_Stephens_and_Wiens_2003_ / not_closeable or_closeable, 60
Anterior_plastron_Burke_et_al_1996_Stephens_and_Wiens_2003 / not_closeable or_closeable, 61
Seams_of_plastral_bones_Stephens_and_Wiens_2003 / not_visible
or_visible_through_plastral_scutes, 62
Seams_of_plastral_scutes_Minx_1996_Stephens_and_Wiens_2003_Burroughs_et_al /
not_darker_than_scutes or_darker_than_scutes, 63
Markings_on_plastron_Stephens_and_Wiens_2003 / absent_scutes_of_plastron_monotone
or_present, 64
Markings_on_plastron_when_present_Stephens_and_Wiens_2003_Within_the_species_scored_as_3
_some_individuals_would_exhibit_a_combination_of_1_and_2_while_other_individuals_of_the_sa
me_species_would_exhibit_a_combination_of_0_1_and_2_Thus_the_various_specimens_scored_as
_3_seemed_to_be_exhibiting_homologous_states_of_this_character /
consist_of_dark_markings_on_a_light_background or_light_markings_on_a_dark_background, 65

Markings_of_plastron_when_present_Stephens_and_Wiens_2003 /
located_on_lateral_edges_of_plastron
in_the_middle_of_individual_plastral_scutes_not_contacting_edges
along_central_axis_of_plastron_spreading_along_seams_of_plastron
or_occur_in_at_least_two_of_the_above_locations, 66
Plastral_markings_when_present_Seidel_&_Palmer_1991_Stephens_and_Wiens_2003 /
consist_of_a_single_dark_figure or_iso '-' _lated_markings_that_are_not_interconnected, 67
Male_plastron_Minx_1996_Stephens_and_Wiens_2003_Joyce_and_Bell_2004_Burroughs_et_al /
flat or_bearing_concavity, 68
Concavity_of_male_plastron_when_present_Stephens_and_Wiens_2003 /
restricted_to_posterior_half_of_plastron or_extends_along_entire_length_of_plastron, 69
Gulars_in_ventral_view_Stephens_and_Wiens_2003 / flush_with_anterior_margin_of_humerals
or_extend_anteriorly_to_margin_of_humerals, 70
Humoral_pectoral_seam_Gaffney_&_Meylan_1988_Stephens_and_Wiens_2003_Joyce_and_Bell_2
004_Burroughs_et_al / does_not_contact_or_is_posterior_to or_contacts_entoplastron, 71
Contour_of_pectoral_abdominal_seam_Gaffney_&_Meylan_1988_Stephens_and_Wiens_2003 /
horizontal or_sloped_posteromedially_to_approach_abdominofemoral_seam, 72
Contour_of_anterior_apex_of_femoral_anal_seam_Stephens_and_Wiens_2003 / acute
or_smooth_curving_line, 73
Notch_at_lateral_edge_of_femoral_anal_seams_Stephens_and_Wiens_2003 / absent or_present, 74
Posteromedial_margin_of_plastron_Seidel_1994_Stephens_and_Wiens_2003 /
curved_anteromedially consists_of_deep_V_shaped_indentation_between_posterior_anals
forms_a_horizontal_line or_rounded_posteriorly, 75
Anterior_margin_of_plastron_Stephens_and_Wiens_2003 / not_serrate or_serrate, 76
Posterior_margin_of_plastron_Stephens_and_Wiens_2003 / not_serrate or_serrate, 77
Inguinal_scute_Minx_1996_Stephens_and_Wiens_2003 / absent or_present, 78
Inguinal_scute_Minx_1996_Stephens_and_Wiens_2003_Burroughs_et_al /
with_smooth_surface_growth_rings_not_visible or_with_visible_growth_rings, 79
Inguinal_scute_Seidel_1994_Stephens_and_Wiens_2003 / unmarked or_bearing_black_markings,
80
Apical_scale_Minx_1996_Stephens_and_Wiens_2003_Burroughs_et_al_In_the_latter_case_the_apic
al_scale_is_small_and_elongate / absent or_present, 81
Apical_scale_Minx_1996_Stephens_and_Wiens_2003_Burroughs_et_al_when_present /
with_visible_growth_rings or_not_cornified_and_with_no_visible_growth_rings, 82
Axillary_scute_Minx_1996_Stephens_and_Wiens_2003_Burroughs_et_al / absent or_present, 83
Bridge_of_plastron_a_dorsal_extension_of_the_plastron_that_is_visible_externally_and_contacts_th
e_carapace_Stephens_and_Wiens_2003 / absent or_present, 84
Markings_on_bridge_Stephens_and_Wiens_2003 / absent
or_present_consisting_of_an_elongate_black_blotch_or_thick_black_line, 85
Dark_markings_on_underside_of_some_or_all_marginals_Stephens_and_Wiens_2003 / absent
or_present, 86 Dark_markings_under_marginals_if_present_Stephens_and_Wiens_2003 /
occur_on_all_marginals on_marginals_near_bridge_only
or_on_all_marginals_near_bridge_and_anterior_to_bridge, 87

Number_of_emergent_hind_claws_Minx / four or_three_, 112 Hind_foot_webbing_Burke_et_al / _absent_or_extending_only_to_proximal_margin_of_claws_ or_extending_nearly_to_distal_end_of_claws_, 113 Clasping_claws_Minx / _absent_ or_present_, 114 Scales_on_the_forelimbs_Minx / _relatively_flat_ or_convex protruding_outward_and_appearing_bulbous_or_rugose_, 115 Color_of_scales_on_forelimbs / _same_as_that_of_skin_on_forelegs_ or_different_from_colour_of_skin_on_forelegs_, 116 Scales_on_outer_edge_of_forelimbs / _serrate_ or_not_serrate_, 117 Stripes_on_forelimbs / _absent_ or_present_, 118 Number_of_stripes_on_forelimb, 119 Posterior_surface_of_hindlimb / _unmarked_ or_marked_with_stripes_or_spots_, 120 Shape_of_the_fissura_ethmoidalis_modified_from_Crumly_1982_13_Hirayama_1985_1_McCord_et_al_1995_5 / _narrow_or_closed_keyhole_shaped_Fig_1 very_wide_Fig_2_, 121 Medial_inflection_of_the_inferior_descending_processes_of_the_frontal_modified_from_Hirayama_1985_2 / absent_or_very_small_Fig_3 present_well_developed_medial_contact_present_or_almost_present_Fig_4_, 122 Frontal_contribution_to_the_orbital_rim_modified_from_Crumly_1982_17_Hirayama_1985_3_Shaffer_et_al_1997_97_Yasukawa_et_al_2001_1 / 'present, no prefrontal/postorbital contact on dorsal surface' 'absent, frontal excluded from orbital rim by prefrontal/postorbital contact', 123 Contact_between_jugal_and_pterygoid_modified_from_Hirayama_1985_11_12_McCord_et_al_1995_3_Burke_et_al_1996_23_Yasukawa_et_al_2001_4_5 / present_medial_process_of_jugal_well_developed_and_touching_the_pterygoid_Fig_7 absent_medial_process_reduced_Fig_8_, 124 Contact_of_the_inferior_process_of_the_parietal_with_the_medial_process_of_the_jugal_Hirayama_1985_13 / absent_Fig_13 present_Fig_14_, 125 Contact_of_the_inferior_process_of_the_parietal_with_the_maxilla_Hirayama_1985_14 / absent_Fig_13 present_Fig_14_, 126 Extent_of_quadratojugal_modified_from_Hirayama_1985_16_Shaffer_et_al_1997_47_Burke_et_al_1996_21_McCord_et_al_1995_6_Yasukawa_et_al_2001_7_8 / quadratojugal_well_developed_firmly_attached_to_jugal_Fig_15 quadratojugal_present_contact_lost_with_jugal_Fig_16 quadratojugal_so_heavily_reduced_that_it_appears_to_be_absent_in_many_skeletal_specimens_Figs_17_18_, 127 Contribution_of_jugal_to_the_rim_of_upper_temporal_emargination_Hirayama_1985_15 / absent_Figs_19_20 present_Fig_21, 128 Contact_between_the_quadratojugal_and_the_articular_facet_of_the_quadrate_modified_from_Hirayama_1985_17 / absent_Fig_22 present_quadratojugal_sends_a_process_ventrally_along_the_rim_of_the_cavum_tympani_and_touches_the_lateral_edge_of_the_articular_facet_Fig_23_, 129 Contact_between_quadratojugal_and_maxilla_Hirayama_1985_18 / absent_Fig_22 present_Figs_23_24_, 130 Medial_contact_of_the_maxillae_along_the_anterior_margin_of_the_jaw_modified_from_Hirayama_1985_20_McCord_et_al_1995_2_Yasukawa_et_al_2001_10 / absent_Figs_25_26 present_Fig_27_, 131 Size_of_the_foramen_orbito_nasale_modified_from_Hirayama_1985_33_Gaffney_and_Meylan_198

8_F93_F102_G103_H111_H163_Crumly_1982_25_Crumly_1994_12 /
small_less_than_onesixth_of_orbit_length_Figs_28_29
large_more_than_onesixth_of_orbit_length_Fig_30_, 132
Contact_between_maxilla_and_vomer_0_Hirayama_1985_31_Crumly_1982_21_Yasukawa_et_al_2001_14 / _present_Fig_31 absent_vomer_separated_from_the_maxilla_by_the_premaxilla_Fig_32_, 133
Size_of_the_foramen_palatinum_posterius_modified_from_Hirayama_1985_22_Gaffney_and_Meylan_1988_F22_F61_McCord_et_al_1995_4_Yasukawa_et_al_2001_12 / large_Fig_33
small_Fig_34_, 134 Position_of_the_pterygoid_relative_to_foramen_palatinum_posterius_ /
pterygoid_situated_posterior_to_the_fpp_Fig_33
pterygoid_situated_posterior_to_the_fpp_but_sends_a_process_anterior_and_lateral_to_the_fpp_Fig_34, 135 Epipterygoid_participation_in_the_trigeminal_foramen_ / absent_Fig_35
present_epipterygoid_clearly_separates_the_parietal_and_pterygoid_in_lateral_view_Fig_36, 136
Development_of_the_foramen_praepalatinum_as_a_canal_canalis_praepalatinum_that_is_concealed_by_a_bony_secondary_palate_in_ventral_view_modified_from_Hirayama_1985_24 /
absent_Fig_39 present_Fig_40_, 137
Contact_between_pterygoid_and_basioccipital_modified_from_Gaffney_and_Meylan_1988_F11_F103_H183_Crumly_1994_Shaffer_et_al_1997_103 / present_Fig_41 absent_Fig_42_, 138
Contact_of_the_pterygoid_with_the_articular_facet_of_the_quadrate_Hirayama_1985_38 /
absent_Fig_43 present_Fig_44_, 139
Closure_and_depth_of_the_incisura_columella_auris_Crumly_1985_Gaffney_and_Meylan_1988_H13 / absent_incisura_is_open_Fig_44 present_incisura_closed_Fig_45_, 140
Angular_contribution_to_the_sulcus_cartilaginis_Meckelii_modified_from_Gaffney_and_Meylan_1988_F14 /
present_the_angular_contributes_to_the_sulcus_and_is_as_long_or_longer_than_the_prearticular_Fig_47 absent_the_angular_is_shorter_than_the_prearticular_Fig_48_, 141
Contact_between_surangular_and_dentary_Crumly_1982_12_Crumly_1985_Gaffney_and_Meylan_1988_H61 / simple_contact_Fig_49 strongly_interdigitated_suture_Fig_50_, 142
Height_of_the_processus_coronoideus_modified_from_Hirayama_1985_45 /
as_high_as_dentary_Fig_51 rising_significantly_above_the_dentary_Fig_52_, 143
Foramen_dentofaciale_majus_Hirayama_1985_47 / small_Fig_53
large_and_situated_within_a_large_lateral_fossa_Fig_54_, 144
Participation_of_palatine_in_the_triturating_surface_of_the_upper_jaw_Hirayama_1985_26_Gaffney_and_Meylan_1988_F21 / absent_Fig_55 present_Figs_56_57_, 145
Participation_of_the_vomer_in_the_triturating_surface_of_the_upper_jaw_Hirayama_1985_25 /
absent_Figs_56_57_58 present_Fig_59_, 146
Presence_and_number_of_lingual_ridges_of_the_triturating_surfaces_of_the_upper_and_lower_jaws_modified_from_Hirayama_1985_29_44_Gaffney_and_Meylan_1988_F72_F91 /
no_lingual_ridges_present_Fig_60 one_lingual_ridge_present_Figs_61_62
two_lingual_ridges_present_, 147
Well_developed_serrations_on_labial_or_lingual_ridges_of_the_triturating_surfaces_of_the_upper_and_lower_jaws_modified_from_Hirayama_1985_21_27_41_43_46_Gaffney_and_Meylan_1988_F92_Yasukawa_et_al_2001_11 / absent_Fig_60 present_Fig_61_, 148

Median_ridge_or_sulcus_of_the_triturating_surface_of_the_upper_jaw_modified_from_Hirayama_1985_30_Crumly_1985_1994_4_Gaffney_and_Meylan_1988_H31 / both_structures_absent_Fig_60 median_ridge_present_Fig_62 median_sulcus_present_Fig_63_, 149
Posterior_extension_of_the_lower_triturating_surface_behind_the_symphysis_of_the_dentary_Hirayama_1985_42_Gaffney_and_Meylan_1988_G52 / absent_Fig_64 present_Fig_65_, 150
Shape_of_coracoid_blade_Crumly_1985_1994_Gaffney_and_Meylan_1988_H17 / long_and_narrow_Fig_131 short_and_very_wide_Fig_131_ 'long and wide (I need to Figure)', 151
Webbing_between_digits_Hirayama_1985_b / present_well_developed_Fig_134 absent_or_at_least_strongly_reduced_Fig_135_, 152
Sexual_size_dimorphism_Gaffney_and_Meylan_1988_F52_Burke_et_al_1996_37 / absent present_female_much_larger_than_male_, 153
Coossification_of_carapacial_bones_modified_from_Minx_1996_character_CO_Burroughs_et_al_In_Press_character_16 / absent_ present_in_more_than_50%_of_the_bones_in_the_carapace, 154
Contact_between_first_vertebral_and_second_marginal_scutes__Hirayama_1985_character_O_Joyce_and_Bell_2004_character_47_Burroughs_et_al_In_Press_character_20 / absent_ present_, 155
Contact_between_the_third_pleural_and_sixth_marginal_scutes_Hirayama_1985_character_B_Joyce_and_Bell_2004_character_48_Burroughs_et_al_In_Press_character_21 / absent_ present, 156
Contact_between_the_fifth_vertebral_and_tenth_marginal_scutes_Hirayama_1985_character_K_and_Joyce_and_Bell_2004_character_46_Burroughs_et_al_In_Press_character_22_ / absent_ present, 157
Twelfth_marginal_scute_Joyce_and_Bell_2004_character_49_Burroughs_et_al_In_Press_character_23_ / two_present_with_their_common_sulcus_partially_dividing_the_pygal_ two_present_but_their_common_sulcus_fully_divides_the_pygal_ twelfth_marginal_scutes_fused_along_the_midline, 158
Presence_of_a_cervical_scute__Joyce_and_Bell_2004_character_40_Burroughs_et_al_In_Press_character_24_ / Absent Present, 159
Position_of_the_anterior_sulcus_of_the_fourth_vertebral_Hirayama_1985_characters_L_and_M_Joyce_and_Bell_2004_character_42_Burroughs_et_al_In_Press_character_29 / sulcus_lies_on_fifth_neural_ sulcus_lies_on_fourth_neural_or_on_the_suture_between_the_fourth_and_fifth_neurals_ sulcus_lies_on_the_sixth_neural_or_on_the_suture_between_the_fifth_and_sixth_neurals, 160
Position_of_the_posterior_sulcus_of_the_fourth_vertebral_Hirayama_1985_characters_L_and_M_Joyce_and_Bell_2004_character_43_Burroughs_et_al_In_Press_character_30 / sulcus_lies_on_the_eighth_neural_or_on_the_homologue_of_the_eighth_neural_ sulcus_lies_on_the_seventh_neural_or_on_the_suture_between_the_seventh_and_eighth_neurals_ eighth_neural_absent_and_sulcus_overlies_costals_that_meet_at_midline, 161
Portion_of_posterior_tip_of_the_gular_scute_extends_onto_entoplastron__Burroughs_et_al_In_Press_character_38 / not_intruded_ intruded, 162
Contact_between_opposite_gular_and_humeral_scutes_Burroughs_et_al_In_Press_character_39_ / no_contact_between_opposite_scutes_ contact_present_, 163
Contact_between_opposite_humeral_and_pectoral_scutes_Burroughs_et_al_In_Press_character_40al_scutes / _no_contact_between_opposite_scutes _left_humeral_scute_contacts_right_pectoral_scute_

_right_humeral_scute_contacts_left_pectoral_scute, 164
Contact_between_opposite_pectoral_and_abdominal_scutes_Burroughs_et_al_In_Press_character_4
1 / no_contact_between_opposite_scutes_ left_pectoral_scute_contacts_right_abdominal_scute_
right_pectoral_scute_contacts_left_humeral_scute, 165
Contact_between_opposite_abdominal_and_femoral_scutes__Burroughs_et_al_In_Press_character_4
2_ / No_contact_between_opposite_scutes left_abdominal_scute_contacts_right_femoral_scute
right_abdominal_scute_contacts_left_femoral_scute, 166
Contact_between_opposite_femoral_and_anal_scutes__Burroughs_et_al_In_Press_character_43_ /
No_contact_between_opposite_scutes left_femoral_scute_contacts_right_anal_scute
right_femoral_scute_contacts_left_anal_scute, 167
Absence_or_Presence_of_Epiplastral_beak_on_the_anterior_lobe_of_the_plastron__modified_from_
Holman_and_Fritz_2005_and_Burroughs_et_al_In_Press_character_49_ / Absent Present, 168
Position_of_the_humero_pectoral_sulcus_with_respect_to_the_anteriorposterior_midline_of_the_ent
oplastron__modified_from_Holman_and_Fritz_2005_Burroughs_et_al_In_Press_character_51 /
Approximately_at_the_midline_of_the_entoplastron_
Sulcus_shifted_significantly_anterior_to_the_midline_of_the_entoplastron_
Sulcus_shifted_significantly_posterior_to_the_midline_of_the_entoplastron_orbital_rim_modified_fr
om_Crumly_1982_17_Hirayama_1985_3_Shaffer_et_al_1997_97_Yasukawa_et_al_2001_1, 169
Concavity_on_the_ventral_surface_of_fused_pelvis / Absent Present, 170
Depth_of_concavity_on_ventral_surface_of_fused_pelvis_when_present / Shallow Deep, 171
Angle_between_acromion_process_and_scapular_process / Approximately_90_degrees
Less_than_90_degrees_ Greater_than_90_degrees, 172 Number_of_pairs_of_peripheral_bones /
10_pairs 11_pairs 12_pairs Less_than_10_pairs Greater_than_12_pairs, 173
Number_of_pairs_of_costal_bones / 7_pairs 8_pairs less_than_7_pairs greater_than_8_pairs, 174
Number_of_pairs_of_marginal_scutes / 10 11 12 less_than_10 greater_than_12, 175
Number_of_vertebral_scutes / 3 4 5 less_than_3 greater_than_5, 176
Number_of_pairs_of_pleural_scutes / 3 4 5 less_than_3 greater_than_5, 177
Presence_of_inframarginal_scutes / Present Absent, 178
Presence_of_coalesence_of_the_femoral_trochanters_on_ventral_surface_of_femur / Absent
Present, 179 Presence_of_costiform_process_on_nuchal / Present Absent ;

MATRIX

Deirochelys_reticularia_OMNH_37928_Deirochelys_reticularia_OMNH_39963
13{0 1}20222222??0211013?1210011???11?1?11000?00?0?00????0{0 1}20000????????10010{0
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Testudo__Geochelone__denticulata_OMNH_39852_Testudo__Geochelone__denticulata_O
MNH_40071 13111{3 4}{0 2}{2 3}2{0 1}22?03111011?1001?01{0 1}{1 2}{0
1}20{0 1}11?{0 1}0?{0 1}0?0?00????{0 3}{1 2}{0 2}{0
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Gopherus_agassizii_OMNH_43874_Gopherus_agassizii_OMNH_40073_Gopherus_agassizii
_OMNH_40072 13{0 1}10{2 4}{0 2}{0 4}{0 2}{0 2}{2 4}{0 2}?0{1 2}1{1 2}102{1

2}12{1 2}0000???1{1 2}?1?1??00?0?????0????{0 3}{1 2}20000????????10{0 1}1110{0
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Gopherus_polyphemus_OMNH_39859_Gopherus_polyphemus_OMNH_40581
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Geochelone_nigra_OMNH_39860_Geochelone_nigra_omnh_40579
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Trachemys_scripta_OMNH_38254
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01???00121???12222 0????????
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Glyptemys__Clemmys__insculpta_OMNH_39962
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Graptemys_geographica_OMNH_39965
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Testudo_graeca_OMNH_40080
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_Geochelone_pardalis_OMNH_39853
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Pseudemys_catespilla_OMNH_34859
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21

Manouria_impressa_OMNH_43875
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Graptemys_pseudogeographica_OMNH_39966_
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Dipsochelys__Aldabrachelys__dussumieri_OMNH_39849
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'Chinemys reevesi TNHC 69388+Chinemys reevesi TNHC 64814+Chinemys reevesi TNHC 64815' 131??????????????11(1 2)1(0 1)210010???1020(0 1)?0000?00?0?011(0 1)0(0 1)(1 2)(0 2)1000000(0 1)031??11(0 1)(0 1)11001000?1100??????????????????????????????????0000110(0 1)10100111001000100000010??00(0 1)0(0 1)1??11120102??1??221

'TMM_40688-93' 00120002222???002????120???????101?????????????11??????0111?????????1010300??????0???? ??0???????1?1?00?2??0?????

Terrapene_carolina_major_CAS_228375 00120222241??000101111221110?101020????00?0?????111??0?01111????????11100300??0?10?? ??????????????????????????????????0001001000100100010?0100000000??0000110211?0202??0 11221

Chelydra_serptina_CAS_228457 0002????????????000000??00110??01?1??????????0??0????1?00000?????????????????????0????? ??????????????????????????????????0000100000010001010110000000001??0????0????????????021?? ?

Chrysemys_picta_TNHC_69404 13010222222??????113112100?0???11?1??1100-011??10----3211000111020?-101003001010-111102??0000?1??11?11202?? ??1221

Terrapene_nelsoni_UTEP_1229 000??????????0101???????????0???2000??1??????????????10?1?????????????????????????0?????? ??00001??????????????1221

_Emys_orbicularis_TNHC_64831 0202??????????3111?111??0010?1?11-01??000-01-1100----12211010010--??0?0002000--0-01?100??????????????????????????????001?00?00000?0000100?0010?00001??0100?1??1121200 ???111221

Emys_orbicularis_TNHC_64832 0201??????????31111111??001001011-1--?000-01-1100----1221101011033??0?1002000--0-11?100??????????????????????????????001??0????0000100100?0010000001??010001??1111100 ?0-111221

Terrapene_corneri_UNSM_21618 ?0??????????????1122122??????????????????????????????????1?1????????110???0?????????????? ??111???12????????

'Emys orbicularis cf. luteofusca D-42967 - See DresdenEmys Measurement Data for locality data' 031??????????????10211??000001011-1-??000-01?0?00---- 3?1111101102311 1?1001000--0-0000--?????????????????????21-0????????00100???000010000000101100000001??1?00????1012010?0-0???21

'Emys trinacris D-46664 - Silician Pond Turtle' 03120222223--011210211??00?001011-1-?-000-01?1101200112101111101003??101000000--0-10----?????????????????????????????????00110000100000000110????00000????010001??111022020-111221

'Ocadia sinensis D-40539 - No Locality data'
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?101?1221
'Morenia (Batagur) petersi D-28068 - Bangladesh Market place'
130??????????120110011??0000110101?????00-0?????0----
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'Melanochelys trijuga D- 38993 - Leipzig zoo specimen'
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'Malayemys subtrijuga from Cambodia, D-42514'
130????????????01211?????????11-11?-----0100-011201001000001100 3??100011000--0-
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'Malayemys subtrijuga D-42522'
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'Notochelys platynota D-41948'
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000?????????????????????????????0????????00?000000000000100001010000000 3??100001??1111221
2--1??241
'Mauremys leprosa D-4762, this specimen survived Allied firebombing. '
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'Mauremys leprosa D-43362'
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'Mauremys iversoni D-40653'
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'Cyclemmys oldhammi shanensis D-40300 - Bangkok Marketplace'
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'Cyclemmys oldhammi shanensis D-40390'
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'Cyclemmys tcheponensis D-44278'
030122222022-0312000112200100001 1-01?1001200-0-0110011011101000---??111100000--0-010??????????????????????22-0????????00100010000000010000101000000 01??00001100111122020-111221

'Cyclemmys atripons D-42549 - potentially subadult based on not quite complete closure of costal fontanelles'130122222022-131100201220000010 01-00?0011201?140110011120101000---??11?110000--0-011104??????????????????22-0????????00100010000000010000100000000 01??0000110011 1?0202??111221

'Cyclemmys atripons/pulchristriata D-42548'
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'Cuora mccordi D-45162'
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'Cuora aurocapitata D-45154'
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'Cuora pani, D-41891' 030122202022-?31200101??00100??11-00-1000-00-0-012201321011001020 0-110000000--0-00-100??????????????????????0????????00100020000000110000000?0000001??000011???110220?--011221

'Cuora zhoui D-45163'
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'Cuora zhoui D-46579'
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'Cuora galbinifrons bourreti D-41868'
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'Cuora galbinifrons bourreti D-40490'
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'Annamemys (Mauremys) annamensis D-40829'
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'Platysternon megacephalum vogeli D-40794'
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Indotestudo_elongata_CMNH_112249
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Rhinoclemmys_punctularia_CMNH_124271
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Indotestudo_elongata_CMNH_125914
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0??121
Rhinoclemmys_punctularia_CMNH_118581
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Rhinoclemmys_punctularia_CMNH_124272
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'Rhinoclemmys (Callopsis) punctularia CMNH 118583'
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Ocadia_sinensis_CMNH_118519
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Ocadia_sinensis_CMNH_118511
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Graptemys_nigrinoda_CMNH_67407
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Ocadia_sinensis_CMNH_66395
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Cuora_flavomarginata_CMNH_87474
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Cuora_flavomarginata_CMNH_113086
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Testudo_graeca_YPM_R_13284
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Testudo_graeca_YPM_R_10594
131??????????????10221??00020??10100?1000-00-1700----1120000001003??1?001000000011100-
-
??????????????????????????????????1011001100011100000100000100001??101021???122011???211
121
Heosemys_spinosa_YPM_R_12608
130??????????????11321??00000--10101?1011010-0-011202020000000103 3??1?0111001000-
110124??????????????????????????????????000100200000001100000000000000??000001???01021
1?--1??221
Testudo_graeca_YPM_R_10599
131???????????0?1111201??000?0--10201?1000-01?1700----1120000????????1??110001000-10-0--
??1??0000-1????????1?--223221
Heosemys_spinosa_YPM_R_13984
13022222224--0412102112200000--11-
?????11?1?????1100?1200000????????1111110??????1?????????????????????????????????000
??0????000001000000000000002??00???1001?11???1--1?1?21
Deirochelys_reticularia_YPM_R_17253
130102222223-041201311210011110101 1-?--00-0-----0----1200000??????0-101012001??0-
11??????????????????????????????????????0010000?000000000101000000000000??0100110011111120
210211221
Deirochelys_reticularia_YPM_R_16033
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11???0??0???????1102220??0
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Rhinoclemmys_funerea_YPM_R_14340
130???????????????01311??001001?11-01?1000-0100-0120003200000000---??1?0100001010-
110104?????????????????????????????????????0010000000?0101000010011000????0??100001???121120
???1??221
Rhinoclemmys_funerea_YPM_R_12174
130104222040-04120131120001000011-01?1?00-
0?????1200?3200000????????1111000??????1?????????????????????????????????????00000000000
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Deirochelys_reticularia_YPM_R_13288
13010222222--0312002112000112?10???1-
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Geochelone_sulcata_YPM_R_11445
13022230302--
12111032121001201011?????????????????????3220000????????10011100??????1?????????????????
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Terrapene_coahuila_TNHC_68950
00020222223--0201?0111?????????11-1-???00-0?????1200?3220111010---??1?0003000--0-1000--
??00000122 1?20120?????1221
Terrapene_coahuila_TNHC_68360
00020402223--0201?011121???????11-1-???00-0?????0----3200111110---??010003000--0-
100???00000122111 0?200??
?11221
'Emydoidea blandingii MSSM 546 (TNHC 85792)'
030???????????????10311????1111011-1???000-01?1100----3220111001003??1??102000--0-1000--
??????????????????????????????????00?000?????0?00?010100?000???00??1100?1???11?220?101??2
21
'Emydoidea blandingii MSSM 547 (TNHC 85793)'
030???????????3111021 1???1111111-1-??000-01?1100----3200111001030??1?0100000--0-
100120?????????????????????????????????????00?0?00?00?0000001010001 00???00??110001???0?0220
?100?1221
Terrapene_coahuila_TNHC_68962
00020222221--0201?011121???????11-1-?-?00-0?????1000?3200111010---??010103000--0-
100???000?0122111011 00??
?11221
Terrapene_coahuila_TNHC_68955
00020222223--1201101112 2???011011-1-?-?00-0?????1200?3100111????????010003000--0-
10???10000102110021 1011
?11221
Malaclemys_terrapin_TNHC_64834
130104040222-111101211??00000??1??00?1?00-0??????????????000010---??1?1010000--0-

110??????????????????????????????????????0000002O??010100?000001001000O1??0????1???111110?
??011???

Graptemys_konhi_TNHC_64860

????????????????????????????0??
????????????????????????????????000???00100101O?10??001?010000?????????????????????????????

Malaclemys_terrapin_litoralis_TNHC_63070

131???????????31?01011210O0?110???00?1?00-???????????01?1000110---
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0???1??111120021O0?????

Graptemys_konhi_TNHC_64818

130???????????0???0121121000001011-1-?-100?1?????1100111000001110 33??101110001000-
110101??0????????????????????????????????0?0100000?1?10?10????1?1100011??000001??1120200
20-111221

'Actinemys "Clemmys" "Emys" marmorata TNHC 64824'

130102223122-13120101122000 0??11-1-?-?00-01011?0----2220000110---??111100000--0-
01?1?7????????????????????????????????????000100000001000001011001000000??01000100112111
02--011221

Gopherus_berlandieri_TNHC_64786

130104031240-011210221220 00?0??10200?1?00-1?????0----0220000????????101101000--0-
01???100100????01101010??000100200 11??000120001101201
2--211121

Gopherus_berlandieri_TNHC_62559

130104040402-0?121022122???????10200--?00-0?????0----0220000????????100111001--0-
11???00112020112210 12??
??1121

Malaclemys_terrapin_TNHC_66501

130????????????????00011?????2110101001000 0-00-0-0112100201000000---??1?1110000--0-0100--
??1000?1???111110?10???221

Testudo_kleinmanni_CAS_228422

13020404040--0?1?1031122000?0???????????00-0?????0----
0???000????????1111110 0??????1???0????????1?110?1????0
???????1??0000?1??11220202??2?1?21

Testudo_kleinmanni_CAS_228426

13020404040--0?1110321220 00????1???????00-0?????0----
????000????????10111100??????1???
??????1??0????1??1112010 2??2?1?21

Rhinoclemmys_pulcherrima_CAS_228355

13022222042--1???1021120000????10200???00-110???1110?0110000????????111110000--0-
110101???10101102110021 02??
111221

'Pyxidea (Cuora) mouhotii CAS 228365'

020???????????0???11011??001001010001?0000-10-0-011000022111100100 3??100110000--0-

000100??????????????????????????????????0011000000000110100100010000000??10000?????1?110
???2??221

Geoemyda_spengleri_spengleri_CAS_228343

130122221311-03120101121001O???11-1??0?00-1?????1100?1210000????????111110000--0-
01???0001002O??000111000010110000001??000001000122210
2??011221

Cyclemys_dentata_CAS_228333

03022242022--131100311210000?q?11?00?1?00-
1?????1200?0120101????????0110100??????0?????????????????????????????????????00100000000
000000001001100000001??000011??11?01102??101221

Testudo_kleinmanni_CAS_228431

130104220402-0311113212100O2???10200?1?00-0?????0----0???000????????1011110010-0-
11???1??0????10011210202??2
?1?21

Emys_orbicularis_CAS_228347

020?????????????01211?1100211011-1-?-000-0101101200132101110110O3??011100000--0-
000100??0??110001??1102010210
0??221

Notochelys_platynota_CAS_228450

130???????????31200111??0000???01-00??00121101301110202200000010O3??1?1000001000-
010100??????????????????????????????????00100000000000010001001100000000??000011???12111
0???0??241

Emydoidea_blandingii_CAS_228373

??0103122222-1311??????????1???11-1-?-?00-
0?????1200?0200??
????????????????????01000100???????????11221

Rhinoclemmys_pulcherrima_CAS_228377

13022222104--1312102112000100--10100-1?00-
0?????1110?0000000????????1110100??????1?????????????????????????????????????00100020???
000110100001100100000??000001001102110O??111221

'Agrionomys (Testudo) horsfieldii CAS 228398'

13020404042--00121012121000????10000?1?00-0?????0----0200000????????111100000--0-
01?????????????????????????????????????1101000000001110100100000020001??0000?10110222002
2??211121

Siebenrockiella_crassicollis_CAS_228335

13020312222--0412012112000000101001-???00-1?????1100?3100000????????1101110010-0-
11???000000000000000000000011000000??001011001121200
20-011222

Cyclemys_tcheponensis_CAS_228363

03022222202--0412002112200000--11-1-???00-
1?????1100?2120101????????1110000??????1???
??????????01??????0??000011000112110O??011221

Testudo_horsfieldi_CAS_228399
13020404042--0111101012200??????00200???00-0?????0----0100000????????111101000--0-
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211121
Deirochelys_reticularia_CAS_228388
13020222222--0411011112000112???1021????00-0?????0----0200000????????1001100010-0-
11?????????????????????????????????????00?10000001100000100000100000000??00???1001100020
2??011?21
Emydoidea_blandingii_CAS_228346
??0102222222-1311??????????1???1021-1-000-01?1100----0200?????????????????????????0--
??0100010??????????11221
Emydoidea_blandingii_CAS_228448
??0104022222-1311??????????1???1021-1-?00-0?????0----
0200??
????????0100010??????????11221
Testudo_graeca_CAS_228435
13020404042--0312101212200??????10200?1?00-0?????0----0120110????????111101000--0-
01???1??0010?101111112??
211121
Cuora_amboinensis_CAS_228345
02022222221--1201002112100l0???1020111000-
0??0??1100?010?111????????1101130??????0??????????????????????????????????00000000000
0101000010011000000??0000110211000002??111221
Pyxidea_mouhotii_CAS_228444
020???????????0?110111122000????1000111?00-1?????1100?0110111????????110111000--0-
00?????????????????????????????????????1001000000000110100000000000010??100011??1011120
0??1??221
Pseudemys_texana_CAS_228438
130102222222-031200011200007110l???????00-1?????????????000????????00111100l0?0-
11?????????????????????????????????????000000000001010010001001101101O??0????1??1110210
20-0112??
Pyxidea_mouhoutii_CAS_228374
020103220222-0312011112200000101000???00-1?????1100?0100111????????111000000--0-
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0??1?1221
Malaclemys_terrapin_CAS_228340
13000402222200412010112200l0???11?0011000-01013?1110?02000001?0---??101100000--0-01-
??????????????????????????????????????000000001001011010000011100001l??000001001???2002??
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Ocadia_sinensis_CAS_228339
130102222222-0312103112100l0???101--11?00-0?????1100101200000001013??0101110012??0-
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0??111221

Trachemys_scripta_scripta_CAS_228436
13020222222--131101311200000110101l-?-?00-0?????0----
1000000????????000??000??????1?????????????????????????????????????000000?0??01010011??10
111011010??000001021O?0220210011221
Clemmys_guttata_228386
13020222222--03120121122000???????1-???00-0?????????????000????????011100000--0-
01???0??00000100111020002??
111221
Malayemys_subtrijuga_CAS_228445
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0?????1100?21??000????????10011100??????1?????????????????????????????????00001101110
0011?10100011110001O??0000110011??0202??011221
Chrysemys_picta_CAS_228385
130102222222-01120121120000????1??????00-
0??????????02??000????????10011000??????1???
?10?100000??????00??0000010011?11?02??111221
Malayemys_subtrijuga_CAS_228446
130102204024-01110101121000???1???????00-
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00110101O??11100001O??0000010011????02??011221
Cuora_galbinifrons_CAS_228360
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0???????????????111????????0100030???
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Testudo_horsfieldii_CAS_228425
13004031222--03121032120O0????????01???00-0?????0----
02??000????????11111200??????1???
??????1??0000-10011011112??211121
Malaclemys_terrapin_terrapin_CAS_228387
131102222222-03110101122000???1??10???00-
0?????1110????1000????????10011000??????1???
?????????????????1??0000?1001?????02??111?21
'Pseudemys texana M-8284'
131102222222-11120121120000????1???????00-
0?????1200?00??000????????10101000??????1???
??????????????????0??00100100110111O2??011221
'Pseudemys texana M-9960'
13120022222--11120121120000????1??1-???00-
0?????1200?01??000????????10101000??????1???
??????????????????0??0000010O1?????02??011221
'Pseudemys texana M-9966'
131102222222-01120121120000????1??1-?-?00-0?????0-----

???000????????10111000??????1??????????????????????????????????????00000020--
0101001100000100110002??0000010011011102??011221
'Pseudemys texana M-12100'
131102222222-0311012112000??????1???????00-00????0----
0???000????????10111000??????1????????????????????????????????????0000020000101001100000010010000??0000010000121102??011221
'Clemmys guttata M-9196'
130102222222-0312100112222??1100???????00-0?????0----
2???000????????11110200??????1??0000012011022100-?11221
'Clemmys guttata M-9193' 13020222222--
01120001121000???1??1?????????????????????000????????01100000??????1??0??00??010011???102??011221
'Clemmys guttata M-9197' 13022222222--0112110112100?0???1???????00-0?????0----
????000????????01111000??0??0100011111111202??123221
'Clemmys guttata M-9198' 13020222222--0312110112200000101???????00-
0??????????????000????????01111000??000?????????????0110?1001112??000-111121
'Platysternon megacephalum M-9672'
130??????????????1001122000000011-011??00-00-1101200102000000????????101110000--0-01?????????????????????????????????????0000000-
1100000000011010000000??1000?1??0?????02--011221
'Terrapene ornata M-9878' 00020222203--
0001003112000?0???1???????????????0----0???111????????110103000--0-
?0??0??0000010211002102??011221
'Terrapene ornata M-9877' 00022202223--
0001002112210011100????????????????0----????111????????010103000--0-
?0??000??01?????00??0000012211200102 0-011221
'Terrapene ornata M-9882' 00022202023--
0001001112200?????0??01???00-0?????0----0???111????????110103000--0-
?1??0??0000010211001002??011221
'Terrapene ornata M-9880' 00010402222--
0001002112211011100??01???00-0101400----????111????????010102000--0-
10??????????????????????????????????????000???????0000100000????00000?0??0000010200100202 11011221

'Terrapene carolina M-12135'
0?0??????????????????????????????1000111000-0101401210?0200111?????????????????000--0-
10???100001?????????????
?221
'Terrapene carolina M-12134'
0?0??????????????????????????0???102?????00-
0?????1210?2000111?????????????????????????10???
??????????????????????100001?????????????????221
'Terrapene carolina triunguis M-9876'
00021212230--100100?112200?00100000111?00-0101401210?2100111????????110003000--0-
10???000001111110210??
011241
'Terrapene carolina carolina M-9874'
0?020222223--0201??????????0??????0111000-
0101401110221001007???
??????????????????????1000010?????????????11221
'Terrapene parornata OMNH - 58168'
000??????????021210111227???????1??01???00-
0?????1?10???00111????????0101130??????0???
??????????????????????00?0010111????02????1221
'Apalone_spinifera'
00?20411221--0--0----10-001010001----------00--------000----------000--0-0100--
10?1?????????????????????????????1000000000011000?0001??1?0000012??0?----0--------0-0?-1-0---
101
'Caretta_caretta'
1?11?????????0??1????????00???21?1????00?00?0?00????0100000?????????????????????????1
??????????????????????????????????00110000100001O?1100001111000l???0?011?0?????????????????1
121??1
'Macrochelys temminckii TMM M-6855 (Plastron)+Macrochelys temminckii TMM M-6847
(Shell)+Macrochelys temminckii TMM M-6510
(Skull)'1211?????????0???0011??????0???11?0100000?0??0?01121101000000001020??1??10?00101
11111?????????????????????????????????????00100000000101010001100000000???0?010?0???12?
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END;

APPENDIX 5: MATRICES USED IN ANALYSES

PAUP

#NEXUS
BEGIN DATA;
DIMENSIONS NTAX=40 NCHAR=245;

FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = " 0 1 2 3 4 5 6 7 8 9";

MATRIX

Sternotherus_odoratus
0100100100111011110000010??0101111000102?0101010000010102?0111111110110010100100000
0101001020?0?010000?10??0111100011000010100000012?0011011000110000??????0??1011?11000
0?0000700????02000?11?0101000??0?0?10100010000?11000??00?0100000?0????000????0?

Actinemys_marmorata
0010?000100?10110100011000??100110?1111001111011110111?2111110000000000010110000100
0001011101101102121102011100001100000001012?11?01??1?000?011????110000?0??1?0010100?
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Chrysemys_picta
001?1000101010110000101101102001111020100011100011010110201110010101100101000100
0100101110110111010110101110000110000000101011110011001?0100000100100?1002011?111
10100140?10????0000?01111000100???0?0000?21111010??0111031010100?10110??110110010

Clemmys_guttata
0010?000101010110110111000??100111111010001?10000001?1102011110000000001010110000100
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Deirochelys_reticularia
000001??????112101000101010?1001111000100012?1000?111011120111?010111?0010100?000010
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0012110020021100l??11100011002002000011001100l?1?110?100?0100001012O???1011000?

Emydoidea_blandingii
0010010010011021010001100O??100111112010001010001001?0102011100000010001000010000
0001011101101100O?111101110000111110002111101011100110012111????0????0?0??1011011000
000191700????020010111111100100l?11?111100010101111110000?0100000?0?1??00011000?

Emys_orbicularis
0010?000101?10110110111000??110111100000011110000001100020111000010110100100000011
0001011101001l?001?102011100001l??000000010l1??0101101O?011????0????0?0??2011?11000
0?0191700200102001110111010100?0110111010000??0?01??00400?000001000?1??010????0?

Glyptemys_insculpta
00000?10100100110110111000??2101000130000011112?0000111102011110000000000010010000l
0001011101101111020110011100001100000011010l?11?0010000?111????0????0?0??1100100001
1?0181301102?1?111000111000011001?11?1111001111O?10111070O?0000010?0?1??01101000?

Glyptemys_muhlenbergii
0010?0???????0110101011000??2101001011100011100010010112?0111100000000000101100001
0001011101101l?11211?2011100001100000011O?010???01100?01111????0????0?0???01?101001
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Graptemys_barbouri
110111011O?0000?100?000100??0?0111l000?02010101?1100?11?1011101l?1?1?10100?0?00?010
0010111011011?00?111001110000110000000l001?11010?100010010000111001111001001?01001
1001512011110011000?1110001100??0?00101100100l0?10111020O?0100001011O??110110010

Graptemys_caglei
????????????

000101111011001?000110001110000110000000000000101011000?0100100110?00?0??101100?0
110?151101110212100?110000110 03?0?10?11?0011010?1?1110200?010000111?0??0101100??
Malaclemys_terrapin_littoralis
1111110111111031110000010 0??1101111000001010101101010010001110111111100110100000
100????11010011100?1101011100001100000000?0001?1010?10000?011????0????1?0??101000100
00000?0?0101100101 1??1110001100010?0011100011 0?0?11????200?0100000?000??110110010
Malaclemys_terrapin_terrapin
000101011101 10?1110000010 0??1100111000002010001000 01?1122011111111111010?00000001
0010011101101110001101011100001100000000?0???11000?10000?0110?0?0????1?0??1010101000
1001?1401010002011??1110000110300 00?10110001010?10111020 0?0100000?100??110110010
Pseudemys_concinna
0110100110100011110010010111110111100000001110000001011020111001110101011100010 00
1000101110110111002110001110000110000000000101100011000010100100100100?1111001?10
10110112150021012?000??1110001010200??0011?0011010?1011002101010000101101111011001
1
Pseudemys_gorzugi
??
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2??0???1110001110200?01?0110011010?1111102101010000101101111011001 1
Pseudemys_nelsoni
1110100110 1??0111100000101102111111 0?0001001100011010110101110010101001011000100 01
0001011101101101 0?1100??????????0000000001010110110?0?120100000 0????0?1112001110101
100121600????11000??1110001001110?1001110011000?1011101101010000101100111011001 1
Pseudemys_peninsularis
001010???????0?1110000010111010111103000101110000101011020111001110101010100010001
0001011101101110 0?1100011100001100000001010101000110000101000100????0?1112000?1010
1?00121500210 1?1000?11?10001000??0?000?100011000?10001211110100001011011110110011
Pseudemys_rubriventris
0100100100100011110000011111 21?11110?000101110000 1?11112?0111001110101101100 01?001
0001011101101110001110011100001100000001010101 1?0100010?0100000????0?1112011?1010
1100121600????11000111110001111200?1001111011010?1011102101010000101100111011001 1
Pseudemys_texana
01101??1101?10?1110000?1011121?111?0?0000001?010?001011?20111??11001??00110001??010
0010111011?1110121110??????????00?0?0???1111100?110000?0100110100000?10?10011100011
0116110121011010 00?0010011012000?000110011010?1011102101010000101100111011001 1
Terrapene_carolina_carolina
0000?00000?1101101010110 00??3101111130100010100000010112200001000000000001001000 10
00??011100?000010101020111000010110100111101111001010 0?1111????0????0?0??2020001001
1001313012 00?2101?1111111101103??01?1000000???0?0???10000?0000110?0?1??01010100?
Terrapene_carolina_triunguis
0000?00000?1101101101111100??2101001030000010100000010112100100000000000001001100 10
0?01011110?0100101010201100000001100001101 01?1100101100 11?1????0????0?0??0020001000
1001013012 00 02?0101111011111000 1?0011003000???010?0000700?1000010?0?1??01010100?

Terrapene_coahuila
00100000100110110110111000??21010010?10020111000000111102011110000000001010010001000010111100?000011101020111000011110000111101011001010?0?111????0????0?00?1021011000000130?0?10012101?111111111110001?0011003000???010???00000?0000010?0?1??01010100?
Terrapene_nelsoni
??1010110010100011111????0????0?0??10?0101000100191701200101010111111101103000 1?1103000???1111??00000?0010010?0?1??010????0?
Terrapene_ornata
0000?00000?1100101101110 00??2100010010100011100000010112 1000?10000000000100100010011?000110?000000101?200000000101100 00??0111111001110001001????0????0?0??0110101001100121300????2200?111111110111310 00?1102001110111 1??10000?0010010?0?1??010101 00?
Trachemys_gaigeae
??0111010100?00?0100100100?00?11120?1?1110110115 1?00????1??10??1110001110200?10?0100011010?101110?00?01000?10110????011000?
Trachemys_scripta_elegans
00100001101000111100000101101101111000002 0?1100001010110201110010111000001000 1010101110110?1101011000111000011000000010101111001110001010110010010 0?11010?11100011011215011001?1000?111100011103 10?0000110011010?1111102100010000100101011011001 0
Trachemys_scripta_nebulosa
??0101100111100?010????????????????????????????1???0101 10????0100000100000?1001011?10101101 1?1101200112 00???1010000010200?1?1110001101 1?1111 0600?0100001011 0?0??011000?
Trachemys_scripta_venusta
00100000100??001110010?10110110111100000201110000101011010111111 10101?0000100010001000101110110111 00?11?1????????????0???????1101001110001001 0?000100110?100101011010100115120 1?0011?000000010001110200?10?0110011010?111110200?0100001011 0?0??011000?
Platysternon_megacephalum_TNHC_84704
??0111010??000????0?0??11?0110100?000?0?0110010200??????000101020??01100000 1?01111?100?????0???010????????????????
Rhinoclemmys_Punctularia_
????????????????1101001010 01??0000???0?000000?0?010?00?0122111 1??0000101 0?000001??110??????????????10211????????????001??0010???????????000?00???000????0?0??1020?10000?00?0?0110011220 0??????000?1030???1?0110000?0?0?0?100?????????????????????????????
;
end;

Garli – No Additional Outgroups

#NEXUS
BEGIN DATA;

DIMENSIONS NTAX=38 NCHAR=245;
FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = " 0 1 2 3 4 5 6 7 8 9";
MATRIX
Sternotherus_odoratus
0100100100111011110000010??0101111000102?0101010000010102?0111111110110010100100000
0101001020?010000?10??011110001100001010000001?001101100011000002?????0??1011?11000
0?0000700????02000?11?01010000??0?0?10100010000?11000??00?0100000?0????000????0?
Actinemys_marmorata
0010?000100?10110100011000??100110?1111001111011110111?2111110000000000010110000100010111011011?012110201110000110000000101?11?01??1?000?011????110000?0??1?0010100?10017130110120100???11100000003O?1101?110011010?1?1110001?0000000?001??000001000?
Chrysemys_picta
001?10001010101100001011011020011110201000111000110101102011100101011001010001000100010111011011101011011100001100000001010111100110010?0100000100100?1002011?11110100140?10????0000?01111000100???0?0000?2111101O??01110310101000?10110??110110010
Clemmys_guttata
0010?000101010110110111000??100111111010001?1000000l?1102011110000000001010110000100010111011011?100011201110000110000000110100O?10110001O?011????000000?011201111100000?0171700????0200?1111100001103O?111111100110l0?10?110000?1000010?0?1??01001010?
Deirochelys_reticularia
000001??????1121010001010l0?100111100010001?1000?1110111201l1?010111?0010100?00001000101110O?0101011111001110?????0010010?0?0?011101100001111000000????0?10?1011?10100000121100200211001??11100011002O0?00001100110O1?1?110?100?0100001012O???1011000?00019170O????020010111111100100l?11?111100010101111110000?0100000?0?1??000110000?
Emydoidea_blandingii
0010010010011021010001100O??100111112010001010001001?0102011100000010001000100001000010111011011000?111101110000111100021111010111001100l?111????0????0?0??1011011000000191700????020010111111100100l?11?111100010101111110000?0100000?0?1??000110000?
Emys_orbicularis
0010?000101?10110110111000??110111100000011110000001100020111000010110100100000011000101110100l1?001?102011100001l??00000001011??0101101O?011????0????0?0??2011?110000?0191700200102001110111010100?011011101000???0?01??00400?000001000?1??010????0?
Glyptemys_insculpta
00000?10100100110110111000??2101000130000011l1?000011110201111000000000001001000010001011101101111020110011100001100000011010l?11?0010000?111????0????0?0??1100100001l?01813011O?1?111000111000011001?11?1111001111O?10111070O?0000010?0?1??011010000?
Glyptemys_muhlenbergii
0010?0???????011010101100O??2101001011100011100010010ll?2011110000000000010110000100010111011011?11211?201110000110000000110?010???01100?01111????0????0?0???01?10100110018130020010211111111000?100010011111100011l0?00111000O?0100010?001??01101010?
Graptemys_barbouri
1101110110?0000?100?000100??0?01111000?02010101?1100?11?10111011?1?1?10100?0?00?010

00101110110?00?11100111000011000000001001?11010?10001001000011100111100100?01001
10015120111100110?0?11100011?0?0?00101100100?0?10111020?0100001011??110110010
Graptemys_caglei
??
????????????????????????????????????1101010110??00100100110010?000100110100110115110?11
1011000?01100001102?0?00101100110?0?10111020?0100001011??1101100??
Graptemys_flavimaculata
0000?00??0100021110100010??00011110?0?0101010110101011020111011011101010000000001
00010111011001?00211010111000011000000010111110??110000?0100001110110?100100110100
11111502010210?1?000001100011102?0?00101100?010?10111021000100001011??110110010
Graptemys_geographica
1100?101??10102110000000110??000111100010101010?1101011010111111010101010010100101
00010111011011101211000111000011000000000000110001100?0?1100001000?00020?111010
100?121?01110001100?111000111020??011110011010?1?1110200?0100001012??11011000?
Graptemys_gibbonsi
11011?01000?00?1100000011??000111103000101010110110010010111011011101010010100101
00010111011111?0120100??????????00?0?0010001?10101101?0?0100000?00?11100?00?110?01
10115110111000?1?000111000110??0?10?0110011010?10111060?0100001011??1101100??
Graptemys_nigrinoda
10010000101000211100100100??00011?10101110101000010101?20111011011111010000000001
00010111011001100211000111000011000000000111110011100001010001011011?10010001010
01111151201021002110001110001110200?101?11001101?1111105100010000101?2?110110010
Graptemys_oculifera
0000?00010100021110010010??000111101001100010100101011020111011011101010000000001
00010111011001?00211000111000011000000001111110101101?11101000001100?0?100100000110
11011512010210010000011100011102?0?10101100110?10111011000100001011??1101100??
Graptemys_ouachitensis_ouach
00100000?00010?11100000100??000111103010101010111101011120111011010101010000000101
00010111011111101211000111000011000000001111110001101001010000011000?1001001?101
01101151201111?11000011100011112?0?101?11001101?10111021000100001?110??110110010
Graptemys_ouachitensis_sabin
??????00101??0?11100001100??000?????20100110001?1111110201110010?????????????????????
??0?100?110100?010??00100000?0??10110100011011511 0
111?00110??0101000111020?0?1?11001101?10111020000100001111?0??101100??
Graptemys_pseudogeographica
00?11001100?031100000010??000111103010101110110101011020111011011111010000000101
01010111011011101211000111000011000000000?1?10001100?0100000110110?0001001?1010
11011511011110211?0?11100011?0200??00110001101?1?11102100010000101?0?010110010
Graptemys_pulchra
1101?101100000?11000000100??000111102000101010111100010120111011010111010010100001
00010111010?11?01?11000111000011000000?0001?10001101?0100000?00111100100111100
11011511011110011000?1110001100200?10001000110?1?1110200?0100001?120??1101100??

Graptemys_versa
0?10000?10000031110000010??0001111020 00?0101011010101102011101101010101000000000100010111011001?0001100011100001100000000000001010110000?0100100110?00?0??101110 0?1100?1511011102121000?1100001100 3?0?10?11?0011010?1?1110200?01000011 1?0??0101100??
Malaclemys_terrapin_littoralis
1111110111111031110000010 0??1101111000001010101101010010001110111111100110100000010 0????1101001110 0?1101011100001100000000?0001?1010?10000?011????0????1?0??101000100 00000?0?0101100101 1??1110001100010?0011100011 0?0?11????200?0100000?000??110110010
Malaclemys_terrapin_terrapin
0001010111011 0?1110000010 0??1100111000002010001000 01?1122011111111111010?00000001 0010011101101110001101011100001100000000?0???11000?10000?0110?0?0????1?0??1010101000 1001?1401010002011??1110000110300 00?1011000101 0?1011102 00?0100000?100??110110010
Pseudemys_concinna
0110100110100011110010010111110111100000001110000001011020111001110101011100010000 1000101110110111002110001110000110000000000101100011000010100100100100?1111001?10 1011011215002101 2?000??1110001010200??0011?0011010?1011002101010000101101111101100 1
Pseudemys_gorzugi
??1110011000 00?0100100 1?1?10?11110?1?1000110?161100???? 2??0???1110001110200?01?0110011010?1111102101010000101101111101100 11
Pseudemys_nelsoni
1110100110 1??0111100000101102111111 0?0001001100011010110101110010101001011000100010001011101101101 0?1100??????????0000000001010110110?0?120100000 0????0?1112001110101 10012160 0????11000??1110001001110?1001110011000?1011101101010000101100111011001 1
Pseudemys_peninsularis
001010???????0?1110000010111010111103000101110000101011020111001110101010100010001 0001011101101110 0?1100011100001100000000101010100011000010100010 0????0?1112000?1010 1?0012150021 01?1000?11?10001000??0?000?10001100 0?1000121111010000101101111011001 1
Pseudemys_rubriventris
0100100100100011110000011111 21?11110?0001011100001?11112?0111001110101101100 01?001 0001011101101110001110011100001100000001010101 1?0100010?0100000 0????0?1112011?1010 1100121600????1100011111000111120 0?1001111011010?1011102101010000101100111011001 1
Pseudemys_texana
01101??1101?10?1110000?1011121?111?0?0000001?010?001011?20111??11001??00110001??010 0010111011?1110121110??????????00?0?0???1111100?110000?0100110100000?10?10011100011 0116110121011010 00?0100011012000?0001100110 1?1011102101010000101101111011001 1
Terrapene_carolina_carolina
0000?00000?1101101010110 00??3101111130100010100000010112200001000000000001001000100 00??011100?0000101010201110000101101001111011110010100?1111????0????0?0??2020001001 1001313012 00?2101?1111111101103??01?1000000???0?0???10000?0000110?0?1??01010100?
Terrapene_carolina_triunguis
0000?00000?1101101101111 00??2101001030000010100000010112100100000000000001001100 10

0?01011110?0100101010201100000001100001101017110010110011?1????0????0?0??0020001000
1001013012000 2?0101111011111000 1?0011003000???010?0000700?1000010?0?1??01010100?
Terrapene_coahuila
0010000010011011011011000??21010010?1002011100000011110201111000000000101001000100
0001011100?0000111010201110000111100001111010110010100?0?111????0????0?00?1021011000
000130?0?10012101?1111111111000 1?0011003000???010???00000?0000010?0?1??01010100?
Terrapene_nelsoni
??
??????????????????????????????????1010110010100011 11????0????0?0??10?0101000100191701200 1
0101011111111011030001?1103000???1111??00000?0010010?0?1??010????0?
Terrapene_ornata
0000?00000?1100101101110000??2100010010100011100000010112100 0?1000000000001001000100
011?000110?000000101?2000000001011000 0??0111111001110001001????0????0?0??0110101001
100121300????2200?1111111101113100 0?1102001110111 1??10000?0010010?0?1??01010100?
Trachemys_gaigeae
??
??????????????????????????????????0111010100?00?0100100100?00?11120?1?1110110115 1?00????
1??10??1110001110200?10?0100011010?101110?00?01000?10110????011000?
Trachemys_scripta_elegans
0010000110100011110000010110110111110000020?1100001010110201110010111000001000 1000
1010101110110?1101011000111000011000000010101111001110001010110010010 0?11010?11100
0110112150110 01?1000?1111000111031 0?0000110011010?1111102100010000100101011011 0010
Trachemys_scripta_nebulosa
??0101100111
00?010?????????????????????????????1???0101107????0100000100000?1001011?10101101 1?110120
011200???1010000010200?1?1110001101 1?1111060 0?0100001011 0?0??011000?
Trachemys_scripta_venusta
0010000010 0??0011100 10?1011011011110000020111000010101101011111110101?0000100010001
0001011101101110 0?11?1????????????0???????1101001110001001 0?000100110?1001010110101 0
0115120 1?0011?0000000100011102 00?10?0110011010?1111102 00?0100001011 0?0??011000?
;
end;

Garli – Additional Outgroups

#NEXUS
BEGIN DATA;
DIMENSIONS NTAX=40 NCHAR=245;
FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = " 0 1 2 3 4 5 6 7 8 9";
MATRIX
Sternotherus_odoratus
0100100100111011110000010 0??0101110001 0?0101010000010 10?0111111110110010100100000

0101001 0?0?010000?10??0111100011000010100000 01?00110110001100000??????0??1011?11000
0?0000700????02000?11?01010000??0?0?10100010000?11000??00?0100000?0????000????0?
Actinemys_marmorata
0010?000100?10110100011000??100110?111100111101111011111?2111110000000000010110000 1
0001011101101 1?012110201110000110000000101?11?01??1?000?011????110000?0??1?0010100?
10017130110120100???1110000000030?1101?110011010?1?1110001?0000000?001??000001000?
Chrysemys_picta
001?100010101011000010110110200111102010001110001101011020111001010110010100010000
10001011101101110101101011100001100000001010111100110010?0100000100100?1002011?111
10100140?10????0000?01111000100???0?0000?21111010??0111031010100 0?10110??110110010
Clemmys_guttata
0010?000101010110110111000??100111111010001?10000001?1102011110000000001010110000 1
0001011101101 1?10001120111000011000000110100 0?10110001 0?011????000000?011201111100
00?0171700????0200?111110000110 30?111111100110 10?10?110000?1000010?0?1??01001010?
Deirochelys_reticularia
000001??????1121010001010 10?10011110001000 1?1000?111011120111?010111?0010100?000010
00101110 0?0101011111001110?????0010010?0?0?0111011000011110000????0?10?1011?101000
0012110020021100 1??11100011002 00?0000110011001?1?110?100?0100001012 0???1011000?
Emydoidea_blandingii
0010010010011021010001100 0??10011111201000101000100 1?0102011100000010001000 1000
0001011101101100 0?111101110000111100021111010111001100 1?111????0????0?0??1011011000
000191700????020010111111100100 1?11?111100010101111110000?0100000?0?1??00011000?
Emys_orbicularis
0010?000101?10110110111000??1101111000000111100000011000201110000101101001000000 11
0001011101001 1?001?10201110000 11??0000000101 1??0101101 0?011????0????0?0??2011?11000
0?0191700200102001110111010100?0110111010000??0?01??00400?000001000?1??010????0?
Glyptemys_insculpta
00000?10100100110110111000??2101000130000011 11?0000111102011110000000000010010000 1
0001011101101111020110011100001100000011010 1?11?0010000?111????0????0?0??1100100001
1?018130110?1?1110001110000110 01?111100111 10?10111070 0?0000010?0?1??01101000?
Glyptemys_muhlenbergii
0010?0???????011010101100 0??2101001011100011100010010 11?2011110000000000010110000 1
0001011101101 1?11211?2011100001100000011 0?010???01100?01111????0????0?0???01?101001
1001813002001021111111000 0?10001001111110001110?00111000 0?0100010?001??01101010?
Graptemys_barbouri
1101110110?0000?100?000100??0?0111100 0?02010101?1100?11?1011101 1?1?1?10100?0?00?010
0010111011011?00?1110011100001100000001001?11010?1000100100001110011110010 01?01001
1001512011110011000?1110001100??0?00101100100 10?10111020 0?0100001011 0??110110010
Graptemys_caglei
??
????????????????????????????????????1101010110 0??0010010011001 0?000100110100110115110 1?11
1011000?0110000110200?00101100110 10?10111020 0?0100001011 0??11011 00??

Graptemys_flavimaculata
0000?00??0100021110100010??00011110?0?0101010110101011020111011011101010000000001
00010111011001?002110101110000110000000101111102?110000?0100001110110?100100110100
11111502010210112?000001100011102002?00101100l?010?1011102100010000101102?110110010
Graptemys_geographica
1100?101??1010211000000110??000111100010101010l?110101101011111101010101001010010l
00010111011011101211000111000011000000000000110001100002?0110000100000?00020?111010
100?121?0111000110002?111000111020022?01111001101012?1?1110200?0100001012022?11011000?
Graptemys_gibbonsi
11011?01000?00?110000000110??000111103000101010110110010010111011011101010010100101
00010111011111?0120100??????????00?0?0010001?10101101002?0100000l?00?11100?00?110?01
10115110111000212000111000111000011000000000111110011100001010001011011002?10010001010
01111151201021002110001110001110200?101?110011010?111110510001000010110??110110010
Graptemys_oculifera
0000?000101000211001001001??00011?10101110101000010101l?2011101101111101000000000l
00010111011001?002110001110000110000000001111110101102111010000011000?100100000110
11011512010210010000011100011102002101011001101012101110110001000010110??11011002?
Graptemys_ouachitensis_ouach
00100000?00010?111000001002?000111103010101010111101011120111011010101010000000101
00010111011111110121100011100001100000000111111000110100101000001100002?1001001?101
01101151201111102110000111000111121002101?110011010?101110210001000012?110??110110010
Graptemys_ouachitensis_sabin
??????00101??0?111000011002?000?????201001100010?111111020111001000000000000000000
??0?100?110100?010??00100000?0??101101000110115110
111?00110??0101000111020020?1?110011010?101110200001000011110???101100??
Graptemys_pseudogeographica
00?110011000?031100000010002?000111103010101110110101011020111011011111010000000101
01010111011011101211000111000011000000000?1?10001100102?0100000110110?0001001?1010
11011511011110211002?111000112?0200??00110001101021?111021000100001011002?010110010
Graptemys_pulchra
1101?101100000?110000001002?000111102000101010111100010120111011010111010010100001
00010111010?11?01?110001110000110000000?0001?10001101102?0100000l?00111100100111100
11011511011110011000?111000110020021000100011010?1?1110200?0100001?120??1101100??
Graptemys_versa
0?10000?10000031110000010002?000111102000?0101011010101102011101101010101000000000l
00010111011001?000110001110000110000000000000101011000002?0100100110?00?0??101110020
110?151101110212100021100001100302?0?10?11?0011010?1?1110200?0100001112?0??0101100??
Malaclemys_terrapin_littoralis
11111101111110311100000100??1101111000001010101101010010001110111111100110100000

100????1101001110?1101011100001100000000?0001?1010?10000?011????0????1?0??101000100
00000?0?0101100101 1??1110001100010?0011100011 0?0?11????200?0100000?000??110110010
Malaclemys_terrapin_terrapin
0001010111011 0?1110000010 0??1100111000002010001000 01?1122011111111111101 0?00000001
0010011101101110001101011100001100000000?0???11000?10000?0110?0?0????1?0??1010101000
1001?1401010002011??1110000110300 00?10110001010?10111020 0?0100000?100??110110010
Pseudemys_concinna
0110100110100011110010010111110111100000001110000001011020111001110101011100010000
1000101110110111002110001110000110000000000101100011000010100100100100?1111001?10
10110112150021012?000??1110001010200??0011?0011010?10110021010100001011011110110011
1
Pseudemys_gorzugi
??
??????????????????????????????????1110011000 0?0100100 1?1?10?11110?1?1000110?161100????
2??0???1110001110200?01?0110011010?1111102101010000101101111011 0011
Pseudemys_nelsoni
1110100110 1??0111100000101102111111 0?0001001100011010110101110010101001011000100 01
0001011101101101 0?1100??????????0000000001010110110?0?120100000 0????0?1112001110101
100121600????11000??1110001001110?1001110011000?10111011010100001011001110110011
Pseudemys_peninsularis
001010???????0?1110000010111010111103000101110000101011020111001110101010100010001
0001011101101110 0?1100011100001100000000101010100011000010100010 0????0?1112000?1010
1?00121500210 1?1000?11?10001000??0?000?100011000?10001211110100001011011110110011
Pseudemys_rubriventris
0100100100100011110000011111 21?11110?0001011100001?11112?0111001110101101100 01?001
0001011101101110001110011100001100000001010101100 0?0100010?0100000????0?1112011?1010
1100121600????1100011111000111120 0?1001111011010?1011102101010000101100111011 0011
Pseudemys_texana
01101??1101?10?1110000?1011121?111?0?0000001?010?001011?20111??11001??00110001??010
0010111011?1110121110??????????00?0?0???1111100?110000?0100110100000?10?10011100011
0116110121011010 0?0010001101200 0?0001100110 10?1011102101010000101100111011 0011
Terrapene_carolina_carolina
0000?00000?1101101010110 00??3101111130100010100000010112200001000000000001001000100
00??011100?0000101010201110000101101001111011110010100?1111????0????0?0??2020001001
1001313012 00?2101?1111111101103??01?1000000???0?0???10000?0000110?0?1??01010100?
Terrapene_carolina_triunguis
0000?00000?1101101101111100??2101001030000010100000010112100100000000000001001100100
?0101111 0?0100101020110000000110000110101?1100101100 11?1????0????0?0??0020001000
1001013012 0002?0101111011111 0001?0011003000???010?0000700?1000010?0?1??01010100?
Terrapene_coahuila
0010000010011011011011000??21010010?1002011100000011110201111000000000101001000100
0001011100?0000111010201110000111100001111010110010 0?0?111????0????0?00?1021011000
000130?0?10012101?1111111111 0001?0011003000???010???00000?0000010?0?1??01010100?

Terrapene_nelsoni
????????????

Sternotherus_odoratus
0100100100111011110000010??0101111000 10?0101010000101 0?0111111110110010100100000
0101001 0?0?010000?10??0111100011000010100000 01?001101100011000 00??????0??1011?11000
0?0000700????02000?11?0101000??0?0?101000100 00?11000??00?0100000?0????000????0?
Actinemys_marmorata
0010?000100?10110100011000??100110?111100111101111011111?2111110000000000010110000 1
000101110110 11?012110201110000110000000101?11?01??1?000?011????110000?0??1?0010100?
10017130110120100???111000000030?1101?110011010?1?1111001?0000000?001??00001000?
Chrysemys_picta
001?100010101011000010110110200111102010001110001101011020111001010110010100010001000
1000101110110111010110101110000110000000101011110011001 0?0100000100100?1002011?111
10100140?10????0000?01111000100???0?0000?21111010??0111031010100 0?10110??110110010
Clemmys_guttata
0010?000101010110110111000??100111111010001?10000001?1102011110000000001010110000 1
000101110110 11?100011201110000110000000110100 0?10110001 0?011????000000?011201111100
00?0171700????0200?111110000110 30?111111100110 10?10?110000?1000010?0?1??01001010?
Deirochelys_reticularia
000001??????112101000101010?100111100010001?1000?111011120111?010111?0010100?000010
0010111 00?0101011111001110?????0010010?0?0?011101100001111000 00????0?10?1011?101000
0012110020021100 1??111000110200?00001100110 01?1?110?100?0100001012 0???1011000?
Emydoidea_blandingii
0010010010011021010001100 0??100111112010001010001001?0102011100000010001000 10000
0010111011011000?111101110000111100021111010111001100 1?111????0????0?0??1011011000
000191700????020010111111100 1001?11?111100010101111110000?0100000?0?1??00011000?
Emys_orbicularis
0010?000101?10110110111000??110111100000011110000001100020111000010110100100000011
0001011101001 1?001?10201110000 11??000000010 11??0101101 0?011????0????0?0??2011?11000
0?0191700200102001110111010100?0110111010000??0?01??00400?000001000?1??010????0?
Glyptemys_insculpta
00000?10100100110110111000??2101000130000011 11?000011102011110000000000010010000 1
0001011101101111020110011100001100000011010 1?11?0010000?111????0????0?0??1100100001
1?0181301 10?1?111000111000011001?11?1111001111 0?10111070 0?0000010?0?1??01101000?
Glyptemys_muhlenbergii
0010?0???????0110101011000??2101001011100011100010010 11?2011110000000000010110000 1
0001011101101 1?11211?201110000110000000110?010???01100?01111????0????0?0???01?101001
1001813002001021111111 1000?1000100111111000111 0?0011100 00?0100010?001??011010 10?
Graptemys_barbouri
1101110110?0000?100?000100??0?0111100 0?02010101?1100?11?1011101 1?1?1?10100?0?00?010
0010111011011?00?111001110000110000000 1001?11010?1000100100001110011110010 01?01001
1001512011110011000?1110001100??0?00101100100 10?10111020 0?0100001011 0??110110010
Graptemys_caglei
??

????????????????????????????????1101010110??001001001100l0?000100110100110115l101?11
1011000?011000011020l?001011001101O?10111020l?010000101l0??11011l00??
Graptemys_flavimaculata
0000?00??0100021110100010l??0001111O?0?0101010110101011020111011011101010000000001
000101111011001?002110101110000110000000101111102??110000?0100001110110?100100110100
1111150201021011?000001100011102l0?00101100l?010?101110210001000010110??110110010
Graptemys_geographica
1100?101??10102110000000110??000111100010101010l?110101101011111101010l0100101001
000101110110111012110001110000110000000000001100011000?0110000100000?00020?111010
100?121?011100011000?111000111020l??011110011010?1?1110200?0100001012O??11011000?
Graptemys_gibbonsi
11011?01000?00?110000000110??000111103000101010110110010010111011011101010010100101
000101110111111?0120100??????????00?0?0010001?10101101l0?0100000l?00?11100?00?110?01
10115110111000210?000111000110O??0?10?0110011010?10111060O?0100001011O??1101100??
Graptemys_nigrinoda
1001000010100021110010010O??00011?10101110101000010101l?20111011011111010000000001
000101110110011002110001110000110000000001111100111000010100010110110?10010001010
011111512010210021100011100011102O0?101?11001101O?111110510001000010110??110110010
Graptemys_oculifera
0000?000101000211100100100??000111101001100010100101011020111011011101010000000001
000101110110O1?002110001110000110000000011111101011O?111010000011000O?100100000110
110115120102100100000111000111020O?10101100110l0?10111011000100000101l0??1101100??
Graptemys_ouachitensis_ouach
00100000?00010?11100000100??000111103010101010111101011120111011010101010000000101
000101110111111012110001110000110000000011111100011010010100000110000?1001001?101
011011512011110?11000011100011112l0?101?11001101O?10111021000100001?110??110110010
Graptemys_ouachitensis_sabin
??????00101??0?11100001100??000?????2010011000l0?111111020111001O??????????????????
??????????????????????????????????????0?100?110100?010??00100000?0??101101000110115110
111?00110??0101000111020O?0?1?11001101O?10111020000100001111O???101100??
Graptemys_pseudogeographica
00?110011000?03110000001002?000111103010101110110101011020111011011111010000000101
010101110110111012110001110000110000000000?1?10001100l0?0100000110110?0001001?1010
110115110111102110O??11100011?0200??00110001101O?1?11102100010000101l0??010110010
Graptemys_pulchra
1101?101100000?110000000100??000111102000101010111100010120111011010111010010100001
000101110l0?11?01?110001110000110000000?0001?10001101l0?0100000l?00111100100111100
110115110111110011000?111000110020O?10001000110l0?1?1110200?0100001?120??1101100??
Graptemys_versa
0?10000?10000031110000010O??000111102000?0101011010101102011101101010101000000001
000101110110O1?000110001110000110000000000001010110000?0100100110?00?0??1011100?0
110?151101110212100O?110000110O3?0?10?11?0011010?1?1110200?0100001110?0??0101100??

Malaclemys_terrapin_littoralis
11111101111110311100000100??1101111000001010101101010010001110111111100110100000
100????110100111001?1101011100001100000000?0001?1010?10000?011????0????1?0??101000100
00000?0?0101100101l??1110001100010?0011100011 0?0?11????200?0100000?000??110110010
Malaclemys_terrapin_terrapin
00010101110110?11100000100??1100111000002010001000 01?1122011111111111010?00000001
00100111011011100011010111000011000000 0?0???11000?10000?0110?0?0????1?0??1010101000
1001?1401010002011??1110000110300 00?10110001010?10111020 0?0100000?100??110110010
Pseudemys_concinna
01101001101000111100100101111101111000000011100000010110201110011101010111000100 0
10001011101101110021100011100001100000000001011000110000101001001001 00?1111001?10
10110112150021012?000??1110001010200??0011?0011010?10110021010100001011011110110011
1
Pseudemys_gorzugi
??
????????????????????????????????????1110011000 0?0100100 1?1?10?11110?1?1000110?161100????
2??0???11100011102 00?01?011001101 0?1111102101010000101101111011 0011
Pseudemys_nelsoni
11101001101??011110000010110211111 10?0001001100011010110101110010101001011000100 01
00010111011011010?1100??????????0000000001010110110?0?120100000 0????0?1112001110101
100121600????11000??1110001001110?100111001 1000?101110110101000010110011101100 11
Pseudemys_peninsularis
001010???????0?1110000010111010111103000101110000101011020111001110101010100010001
00010111011011100?1100011100001100000001010101000110000101000100????0?1112000?1010
1?0012150021012?1000?11?10001000??0?000?100011000?1000121111010000101101111011 0011
Pseudemys_rubriventris
01001001001000111100000111112 1?11110?000101110000 1?11112?011100111010110110001?001
00010111011011100011100111000011000000010101011?0100010?0100000????0?1112011?1010
1100121600????110001111100011112 00?100111011010?101110210101000010110011101100 11
Pseudemys_texana
01101??1101?10?1110000?1011121?111?0?0000001?010?001011?20111??11001??00110001??010
00101110 11?1110121110??????????00?0?0???1111100?110000?0100110100000?10?10011100011
011611012101101000?0010001101200 0?0001100 11010?101110210101000010110111101100 11
Terrapene_carolina_carolina
0000?00000?1101101010110 00??3101111130100010100000010112200001000000000001001000 10
00??011100?0000101010201110000101101001111011110010100?1111????0????0?0??2020001001
1001313012 00?2101?111111110110 3??01?1000000???0?0???10000?0000110?0?1??01010100?
Terrapene_carolina_triunguis
0000?00000?1101101101111 00??2101001030000010100000010112100100000000000001001100 10
0?01011110?0100101010201100000000110000110101?1100101100 11?1????0????0?0??0020001000
1001013012 0002?0101111011111 0001?0011003000???010?0000700?1000010?0?1??01010100?
Terrapene_coahuila
00100000100110110110111000??21010010?1002011100000011110201111000000000101001000 10

000101110?000011101020111000011110000111101011001010?0?111????0????0?00?1021011000
000130?0?10012101?111111111110001?0011003000???010???00000?0000010?0?1??01010100?
Terrapene_nelsoni
??
????????????????????????????????????1010110010100011111????0????0?0??10?0101000100191701200 1
0101011111111011030001?1103000???1111??00000?0010010?0?1??010????0?
Terrapene_ornata
0000?00000?1100101101110000??2100010010100011100000010112100 0?1000000000001001000 10
011?000110?000000101?2000000001011000 0??0111111001110001001????0????0?0??0110101001
100121300????2200?1111111101113100 0?1102001110111 1??10000?0010010?0?1??01010100?
Trachemys_gaigeae
??
????????????????????????????????????0111010100?00?0100100100?00?11120?1?111011011 51?00????
1??10??1110001110200?10?0100011010?101110?00?01000?10110????011000?
Trachemys_scripta_elegans
0010000110100011110000010110110111110000020?1100001010110201110010111000001000 1000
101010111011 0?1101011000111000011000000010101111001110001010110010010 0?11010?11100
011011215011001?1000?1111000111031 0?0000110011010?1111102100010000100101011011 0010
Trachemys_scripta_nebulosa
??0101100111
00?010????????????????????????????????1???010110????0100000100000?1001011?10101101 1?110120
011200???1010000010200?1?111000110 11?11111 0600?0100001011 0?0??011000?
Trachemys_scripta_venusta
00100000100??001110010?1011011011110000020111000010101101011111110101?0000100010001
000101110110111 00?11?1????????????0???????1101001110001001 0?000100110?1001010110101 0
01151201?0011?000000010001110200?10?0110011010?111110200?0100001011 0?0??011000?
;
end;

Bayes – Additional Outgroups

#NEXUS
BEGIN DATA;
DIMENSIONS NTAX=40 NCHAR=245;
FORMAT DATATYPE = STANDARD GAP = - MISSING = ?;
MATRIX
Sternotherus_odoratus
0100100100111011110000010 0??0101111000 10?0101010000010 10?0111111110110010100100000
0101001 0?0?010000?10??0111100011000010100000 01?0011011000110000??????0??1011?11000
0?0000700????02000?11?0101000 0??0?0?10100010000?11000??00?0100000?0????000????0?
Actinemys_marmorata
0010?000100?1011010001100 0??100110?111100111101111011111?2111110000000000010110000 1

0001011101101?012110201110000110000000101?11?01??1?000?011????110000?0??1?0010100?
1001713011012010??111000000030?1101?110011010?1?1110001?0000000?001??00001000?
Chrysemys_picta
001?10001010101100001011011020011110201000111000110101102011100101011001010001000
1000101110110111010110101110000110000000101011110011001O?0100000100100?1002011?111
10100140?10????0000?01111000100???0?0000?2111101O??01110310101000?10110??110110010
Clemmys_guttata
0010?000101010110110111000??100111111010001?10000001?1102011110000000001010110000100
0001011101101?100011201110000110000001101000?10110001O?011????000000?011201111100
00?0171700????0200?1111100001103O?111111100110l0?10?110000?1000010?0?1??01001010?
Deirochelys_reticularia
000001??????112101000101010?100111100010001?1000?11101112011l?010111?0010100?000010
00101110O?0101011111001110?????0010010?0?0?011101100001111000000????0?10?1011?101000
0012110020021100l??11100011002O0?00001100110O1?1?110?100?0100001012O???1011000?
Emydoidea_blandingii
0010010010011021010001100O??100111112010001010001001?0102011100000010001000010000
0001011101101100O?111101110000111100021111010111001100l?111????0????0?0??1011011000
000191700????020010111111100100l?11?111100010101111110000?0100000?0?1??00011000?
Emys_orbicularis
0010?000101?10110110111000??110111100000011110000001100020111000010110100100000011
0001011101001l?001?10201110000l1??00000001011??0101101O?011????0????0?0??2011?11000
0?0191700200102001110111010100?0110111010000??0?01??00400?000001000?1??010????0?
Glyptemys_insculpta
00000?10100100110110111000??2101000130000011l1?0000111102011110000000000010010000l
0001011101101111020110011100001100000011010l?11?0010000?111????0????0?0??1100100001
1?01813011O?1?111000111000011001?11?1111001111O?10111070O?0000010?0?1??01101000?
Glyptemys_muhlenbergii
0010?0???????011010101100O??2101001011100011100010010ll?2011110000000000010110000l
0001011101101l?11211?2011100001100000011O?010???01100?01111????0????0?0???01?101001
1001813002001021111111100O?1000100111111000lll0?00111000O?0100010?001??011010l0?
Graptemys_barbouri
110111011O?0000?100?000100??0?01111000?02010101?1100?11?10111011?1?1?10100?0?00?010
0010111011011?00?111001110000110000000l001?11010?1000100100001110011110010010?01001
1001512011110011000?1110001100??0?00101100100l0?10111020O?0100001011O??110110010
Graptemys_caglei
??
??????????????????????????????????1101010110O??00100100110010?000100110100110115110l?11
1011000?01100001102O0?00101100110l0?10111020O?0100001011O??1101100??
Graptemys_flavimaculata
0000?00??0100021110100010O??00011110?0?0101010110101011020111011011101010000000001
0001011101100l?00211010111000011000000010111110??110000?0100001110110?100100110100
11111502010210ll?000001100011102O0?00101100l?010?10111021000100001011O??110110010

Graptemys_geographica
1100?101??10102110000000110??000111100010101010?1101011010111111010101010010100101
000101111011011012110001110000110000000000001100011000?01100001000007?00020?111010
100?121?011100011000?111000111020??011110011010?1?1110200?0100001012??11011000?
Graptemys_gibbonsi
11011?01000?00?110000000110??000111103000101010110110010010111011011101010010100101
000101111011111?012010??????????00?0?0010001?10101101007?01000001?00?11100?00?110?01
101151101110002 1?000111000110??0?10?0110011010?10111060?0100001011??1101100??
Graptemys_nigrinoda
100100001010002111001001007?00011?10101110101000010101 1?2011101101111101000000001
000101111011001100211000111000011000000000111110011100001010001011011 0?10010001010
011111512010210021100011100011102007101?11001101 0?111110510001000010110??110110010
Graptemys_oculifera
0000?000101000211001001007?000111101001100010100101011020111011011101010000000001
000101111011001?002110001110000110000000011111101011 0?111010000011000 0?100100000110
110115120102100100000111000111020 0?10101100110 10?10111011000100001011 0??1101100??
Graptemys_ouachitensis_ouach
00100000?00010?111000001007?000111103010101010111101011120111011010101010000000101
000101111011111101211000111000011000000001111110001101001010000011000 0?1001001?101
011011512011110?11000011100011112 10?101?11001101 0?10111021000100001?110??110110010
Graptemys_ouachitensis_sabin
?????00101??0?111000011007?000?????2010011000 10?111111020111001 0????????????????????
??0?100?110100?010??00100000?0??101101000110115110
111?00110??0101000111020 0?0?1?11001101 0?10111020000100001111 0???101100??
Graptemys_pseudogeographica
00?110011000?0311000000100??000111103010101110110101011020111011011111010000000101
010101111011011012110001110000110000000000?1?10001100 10?0100000110110?0001001?1010
110115110111102110 0??111000 11?0200??00110001101 0?1?111021000100001011 0??010110010
Graptemys_pulchra
1101?101100000?110000000100??000111102000101010111100010120111011010111010010100001
000101111010?11?01?110001110000110000000?0001?10001101 10?0100000 1?00111100100111100
110115110111110011000?111000110020 0?10001000110 10?1?1110200?0100001?120??1101100??
Graptemys_versa
0?10000?10000031110000010 0??000111102000?0101011010101102011101101010101000000000 1
000101111011001?000110001110000110000000000000101011000 0?0100100110?00?0??1011100?0
110?151101110212100 0?110000110 03?0?10?11?0011010?1?1110200?0100001 11?0??01011100??
Malaclemys_terrapin_littoralis
111111011111103111000001 00??1101111000001010101101010010001110111111100110100000 0
100????1101001110 0?110101110000110000000?0001?1010?10000?011????0????1?0??101000100
00000?0?0101100101 1??1110001100010?00111000110?0?11????200?0100000?000??110110010
Malaclemys_terrapin_terrapin
000101011101107?111000001007??1100111000002010001000017?11220111111111111010?00000001

00100111011011100011010111000011000000?0???11000?10000?0110?0?0????1?0??1010101000
1001?1401010002011??111000011030000?10110001010?10111020?0100000?100??110110010
Pseudemys_concinna
01101001101000111100100101111101111000000011100000010110201110011101010111000100
0
1000101110110111002110001110000110000000000101100011000010100100100100?1111001?10
10110112150021012?000??111000101020??0011?0011010?10110021010100001011011110110011
1
Pseudemys_gorzugi
??
??????????????????????????????????1110011000?0100100 1?1?10?11110?1?1000110?161100????
2??0???111000111020?01?0110011010?111110210101000010110111101100 11
Pseudemys_nelsoni
11101001101??011110000010110211111 10?000100110001101011010111001010100101100010001
0001011101101101 0?1100??????????0000000001010110110?0?120100000????0?1112001110101
100121600????11000??111000100111 0?100111001 1000?101110110101000010110011101100 11
Pseudemys_peninsularis
001010???????0?111000001011101011110300010111000010101102011100111010101010001000 1
0001011101101110 0?1100011100001100000001010101000110000101000100????0?1112000?1010
1?00121500210 1?1000?11?10001000??0?000?100011000?10001211110100001011011110110011
Pseudemys_rubriventris
01001001001000111100000111112 1?11110?000101110000 1?11112?011100111010110110001?001
0001011101101110001110011100001100000001010101 1?0100010?01000000????0?1112011?1010
110012160 0????110001111100011112 00?100111101101 0?101110210101000010110011101100 11
Pseudemys_texana
01101??1101?10?1110000?1011121?111?0?0000001?010?001011?20111??11001??00110001??010
0010111011?111012111 0??????????00?0?0???1111100?110000?0100110100000?10?10011100011
011611012101101000?0010001101200 0?000110011010?101110210101000010110111101100 11
Terrapene_carolina_carolina
0000?00000?1101101010110 00??3101111130100010100000010112200001000000000001001000 10
00??011100?0000101010201110000101101001111011110010100?1111????0????0?0??2020001001
100131301200?2101?111111110110 3??01?1000000???0?0???10000?0000110?0?1??01010100?
Terrapene_carolina_triunguis
0000?00000?1101101101111 00??2101001030000010100000010112100100000000000001001100 10
0?01011110?0100101010201100000000110000110101?1100101100 11?1????0????0?0??0020001000
100101301200 02?0101111011111 0001?0011003000???010?0000700?1000010?0?1??01010100?
Terrapene_coahuila
0010000010011011011011 1000??21010010?1002011100000011110201111000000000101001000 10
0001011100?0000111010201110000111100001111010110010 10?0?111????0????0?00?1021011000
000130?0?10012101?111111111 10001?0011003000???010???00000?0000010?0?1??01010100?
Terrapene_nelsoni
??
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0101011111111011030001?1103000???1111??00000?0010010?0?1??010????0?

Terrapene_ornata
0000?00000?1100101101111000??2100010010100011100000010112100 0?1000000000010010001 0011?000110?000000101?2000000001011000 0??0111111001110001001????0????0?0??0110101001 10012130 0????2200?1111111101113100 0?1102001110111 1??10000?0010010?0?1??01010100?
Trachemys_gaigeae
??? ??????????????????????????????????????0111010100?00?0100100100?00?11120?1?111011011 51?00???? 1??10??1110001110200?10?0100011010?101110?00?01000?10110????011000?
Trachemys_scripta_elegans
0010000110100011110000010110110111110000020?1100001010110201110010111000001000 1000 1010101110110?1101011000111000011000000010101111001110001010110010010 0?11010?11100 0110112150110 01?1000?1111000111031 0?0000110011010?1111102100010000100101010110010
Trachemys_scripta_nebulosa
??0101100111 00?010?????????????????????????????1???01011 0????0100000100000?1001011?10101101 1?110120 011200???1010000010200?1?1110001101 1?111106 00?0100001011 0?0??011000?
Trachemys_scripta_venusta
0010000010 0??001110010?1011011011110000020111000010101101011111110101?0000100010001 0001011101101110 0?11?1????????????0???????1101001110001001 0?000100110?10010101101010 0115120 1?0011?0000000100011102 00?10?0110011010?111110200?0100001011 0?0??011000?
Platysternon_megacephalum_TNHC_84704
??? ??0111010??000????0?0??11?0110100?000?0?0110010 200?????000101020??01100000 1?01111?100?????0???010?????????????????
Rhinoclemmys_Punctularia_
??????????????1101001010 01??0000???0?000000?0?010?00?0122111??0000101 0?00000 1??110?? ???????????10211????????????001??0010???????????000?00???000????0?0??1020?10000?00?0?0 1100112200??????000?1030???1?0110000?0?0?0?100??????????????????????????
;
end;

APPENDIX 6: PAUP AND BAYES BLOCKS

Provided below is a list of PAUP blocks, Bayes blocks, and Garli configuration files used in analyses. Each of these blocks can be combined with their respective matrix from Appendix 5 into a NEXUS file, and executed in their respective programs.

Shell Only Outgroups Added PAUP:

begin paup;

```
   log start replace = yes file = ShellOnlyPAUP_log.txt;
   set autoclose = yes criterion = parsimony root = outgroup storebrlens = yes increase = auto;
   outgroup Sternotherus_odoratus Platysternon_megacephalum_TNHC_84704
Rhinoclemmys_Punctularia_;
   hsearch addseq = random nreps = 100000 swap = tbr hold = 1;
   savetrees file = ShellOnlyPAUP.tre format = altnex brlens = yes;
   log stop;

END;
BEGIN ASSUMPTIONS;
        TYPESET * UNTITLED   =  unord:  1 -  245;

        EXSET * UNTITLED  =  1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188
209 215 221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40
41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72
73 74 75 76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153
154 155;

END;
```

Skull Only Outgroups Added PAUP:

```
begin paup;
   log start replace = yes file = SkullOnly_log.txt;
   set autoclose = yes criterion = parsimony root = outgroup storebrlens = yes increase = auto;
   outgroup Sternotherus_odoratus Platysternon_megacephalum_TNHC_84704
Rhinoclemmys_Punctularia_;
   hsearch addseq = random nreps = 100000 swap = tbr hold = 1;
   savetrees file = SkullOnly.tre format = altnex brlens = yes;
   log stop;

END;
BEGIN ASSUMPTIONS;
        TYPESET * UNTITLED   =  unord:  1 -  245;

        EXSET * UNTITLED  =  1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188
209 215 221-245 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158 159 160
161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 189 190
191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212 213 214
216 217 218 219 220;

END;
```

159 Character Outgroup Added PAUP:

```
begin paup;

   log start replace=yes file=PaupAllCharacters_log_2.txt;
   set autoclose=yes criterion=parsimony root=outgroup storebrlens=yes increase=auto;
   outgroup Sternotherus_odoratus Platysternon_megacephalum_TNHC_84704
Rhinoclemmys_Punctularia_:
   set root=outgroup outroot=mono;
   exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245;
   savetrees file=WiensAllChar_2.tre format=altnex brlens=yes;
   log stop;

END;
```

159 Character Additional Outgroups Removed PAUP:

```
   log start replace=yes file=PaupAllCharacters_log_2.txt;
   set autoclose=yes criterion=parsimony root=outgroup storebrlens=yes increase=auto;
   outgroup Sternotherus_odoratus;
   set root=outgroup;
   delete Platysternon_megacephalum_TNHC_84704 Rhinoclemmys_Punctularia_;
   exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245;
   savetrees file=WiensAllChar_2.tre format=altnex brlens=yes;
   log stop;

END;
```

Shell Characters Only Additional Outgroups Deleted PAUP:

```
begin paup;
   log start replace = yes file = WiensPaupAllCharacters_log.txt;
   set autoclose = yes criterion = parsimony root = outgroup storebrlens = yes increase = auto;
         outgroup Sternotherus_odoratus;
   delete Platysternon_megacephalum_TNHC_84704 Rhinoclemmys_Punctularia_;
   hsearch addseq = random nreps = 100000 swap = tbr hold = 1;
   savetrees file = AllCharacters.tre format = altnex brlens = yes;
   log stop;

END;
BEGIN ASSUMPTIONS;
         TYPESET * UNTITLED   =  unord:  1 -  245;
```

EXSET * UNTITLED = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;

END;

Skull Characters Only Additional Outgroups PAUP:

```
begin paup;
   log start replace = yes file = SkullOnlyOGDelete.txt;
   set autoclose = yes criterion = parsimony root = outgroup storebrlens = yes increase = auto;
   outgroup Sternotherus_odoratus;
hsearch addseq = random nreps = 100000 swap = tbr hold = 1;
   savetrees file = SkullOnlyOGDelete.tre format = altnex brlens = yes;
   log stop;

END;
BEGIN ASSUMPTIONS;
        TYPESET * UNTITLED  =  unord:  1 -  245;

        EXSET * UNTITLED  =  1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188
209 215 221-245 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158 159 160
161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 189 190
191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212 213 214
216 217 218 219 220;

END;
```

Garli – Configuration files

Skull Only with additional Outgroups:

```
[general]
datafname = SkullOnly_withOG_ML.nex
constraintfile =
streefname = random
ofprefix = SkullOnly_withOG_ML
randseed = -1
availablememory = 1000
logevery = 50
```

saveevery = 100
refinestart = 1
outputeachbettertopology = 1
enforcetermconditions = 1
genthreshfortopoterm = 5000
scorethreshforterm = 0.0500
significanttopochange = 0.0010
outputphyliptree = 0
outputmostlyuselessfiles = 0
writecheckpoints = 0
restart = 0
searchreps = 20

datatype=standard
ratematrix = 1rate
statefrequencies = equal
ratehetmodel = none
numratecats = 1
invariantsites = none

[master]
nindivs = 4
holdover = 1
selectionintensity = 0.5000
holdoverpenalty = 0
stopgen = 2147483646
stoptime = 2147483646

startoptprec = 0.5000
minoptprec = 0.0100
numberofprecreductions = 20
treerejectionthreshold = 50.0
topoweight = 1
modweight = 0.0500
brlenweight = 0.2000
randnniweight = 0.1000
randsprweight = 0.3000
limsprweight = 0.6000
intervallength = 100
intervalstostore = 5

limsprrange = 6
meanbrlenmuts = 5
gammashapebrlen = 1000
gammashapemodel = 1000
uniqueswapbias = 0.1000
distanceswapbias = 1

bootstrapreps =
inferinternalstateprobs = 0

Skull only with no additional outgroups:

[general]
datafname = SkullOnly_DelOG_ML.nex
constraintfile =
streefname = random
ofprefix = SkullOnly_DelOG_ML
randseed = -1
availablememory = 1000
logevery = 50
saveevery = 100
refinestart = 1
outputeachbettertopology = 1
enforcetermconditions = 1
genthreshfortopoterm = 5000
scorethreshforterm = 0.0500
significanttopochange = 0.0010
outputphyliptree = 0
outputmostlyuselessfiles = 0
writecheckpoints = 0
restart = 0
searchreps = 20

datatype=standard
ratematrix = 1rate
statefrequencies = equal
ratehetmodel = none
numratecats = 1
invariantsites = none

[master]
nindivs = 4
holdover = 1
selectionintensity = 0.5000
holdoverpenalty = 0
stopgen = 2147483646
stoptime = 2147483646

startoptprec = 0.5000
minoptprec = 0.0100
numberofprecreductions = 20
treerejectionthreshold = 50.0
topoweight = 1
modweight = 0.0500
brlenweight = 0.2000
randnniweight = 0.1000
randsprweight = 0.3000
limsprweight = 0.6000
intervallength = 100
intervalstostore = 5

limsprrange = 6
meanbrlenmuts = 5
gammashapebrlen = 1000
gammashapemodel = 1000
uniqueswapbias = 0.1000
distanceswapbias = 1

bootstrapreps =
inferinternalstateprobs = 0

Shell Only with additional outgroups:

[general]
datafname = ShellOnly_WithOG_ML.nex
constraintfile =
streefname = random
ofprefix = ShellOnly_WithOG_ML

randseed = -1
availablememory = 1000
logevery = 50
saveevery = 100
refinestart = 1
outputeachbettertopology = 1
enforcetermconditions = 1
genthreshfortopoterm = 5000
scorethreshforterm = 0.0500
significanttopochange = 0.0010
outputphyliptree = 0
outputmostlyuselessfiles = 0
writecheckpoints = 0
restart = 0
searchreps = 20

datatype=standard
ratematrix = 1rate
statefrequencies = equal
ratehetmodel = none
numratecats = 1
invariantsites = none

[master]
nindivs = 4
holdover = 1
selectionintensity = 0.5000
holdoverpenalty = 0
stopgen = 2147483646
stoptime = 2147483646

startoptprec = 0.5000
minoptprec = 0.0100
numberofprecreductions = 20
treerejectionthreshold = 50.0
topoweight = 1
modweight = 0.0500
brlenweight = 0.2000
randnniweight = 0.1000
randsprweight = 0.3000

limsprweight = 0.6000
intervallength = 100
intervalstostore = 5

limsprrange = 6
meanbrlenmuts = 5
gammashapebrlen = 1000
gammashapemodel = 1000
uniqueswapbias = 0.1000
distanceswapbias = 1

bootstrapreps =
inferinternalstateprobs = 0

Shell only with no additional outgroups:

[general]
datafname = ShellOnly_DelOG_ML.nex
constraintfile =
streefname = random
ofprefix = ShellOnly_DelOG_ML
randseed = -1
availablememory = 1000
logevery = 50
saveevery = 100
refinestart = 1
outputeachbettertopology = 1
enforcetermconditions = 1
genthreshfortopoterm = 5000
scorethreshforterm = 0.0500
significanttopochange = 0.0010
outputphyliptree = 0
outputmostlyuselessfiles = 0
writecheckpoints = 0
restart = 0
searchreps = 20

datatype=standard
ratematrix = 1rate
statefrequencies = equal

ratehetmodel = none
numratecats = 1
invariantsites = none

[master]
nindivs = 4
holdover = 1
selectionintensity = 0.5000
holdoverpenalty = 0
stopgen = 2147483646
stoptime = 2147483646

startoptprec = 0.5000
minoptprec = 0.0100
numberofprecreductions = 20
treerejectionthreshold = 50.0
topoweight = 1
modweight = 0.0500
brlenweight = 0.2000
randnniweight = 0.1000
randsprweight = 0.3000
limsprweight = 0.6000
intervallength = 100
intervalstostore = 5

limsprrange = 6
meanbrlenmuts = 5
gammashapebrlen = 1000
gammashapemodel = 1000
uniqueswapbias = 0.1000
distanceswapbias = 1

bootstrapreps =
inferinternalstateprobs = 0

Shell only additional outgroups deleted:

[general]
datafname = ShellOnly_withOG_ML.nex

constraintfile =
streefname = random
ofprefix = ShellOnly_withOG_ML
randseed = -1
availablememory = 1000
logevery = 50
saveevery = 100
refinestart = 1
outputeachbettertopology = 1
enforcetermconditions = 1
genthreshfortopoterm = 5000
scorethreshforterm = 0.0500
significanttopochange = 0.0010
outputphyliptree = 0
outputmostlyuselessfiles = 0
writecheckpoints = 0
restart = 0
searchreps = 20

datatype=standard
ratematrix = 1rate
statefrequencies = equal
ratehetmodel = none
numratecats = 1
invariantsites = none

[master]
nindivs = 4
holdover = 1
selectionintensity = 0.5000
holdoverpenalty = 0
stopgen = 2147483646
stoptime = 2147483646

startoptprec = 0.5000
minoptprec = 0.0100
numberofprecreductions = 20
treerejectionthreshold = 50.0
topoweight = 1
modweight = 0.0500

brlenweight = 0.2000
randnniweight = 0.1000
randsprweight = 0.3000
limsprweight = 0.6000
intervallength = 100
intervalstostore = 5

limsprrange = 6
meanbrlenmuts = 5
gammashapebrlen = 1000
gammashapemodel = 1000
uniqueswapbias = 0.1000
distanceswapbias = 1

bootstrapreps =
inferinternalstateprobs = 0

No partitions, with no additional outgroups:

[general]
datafname = NoPart_delOG_ML.nex
constraintfile =
streefname = random
ofprefix = NoPart_delOG
randseed = -1
availablememory = 1000
logevery = 50
saveevery = 100
refinestart = 1
outputeachbettertopology = 1
enforcetermconditions = 1
genthreshfortopoterm = 5000
scorethreshforterm = 0.0500
significanttopochange = 0.0010
outputphyliptree = 0
outputmostlyuselessfiles = 0
writecheckpoints = 0
restart = 0
searchreps = 20

datatype=standard
rematrix = 1rate
statefrequencies = equal
ratehetmodel = none
numratecats = 1
invariantsites = none

[master]
nindivs = 4
holdover = 1
selectionintensity = 0.5000
holdoverpenalty = 0
stopgen = 2147483646
stoptime = 2147483646

startoptprec = 0.5000
minoptprec = 0.0100
numberofprecreductions = 20
treerejectionthreshold = 50.0
topoweight = 1
modweight = 0.0500
brlenweight = 0.2000
randnniweight = 0.1000
randsprweight = 0.3000
limsprweight = 0.6000
intervallength = 100
intervalstostore = 5

limsprrange = 6
meanbrlenmuts = 5
gammashapebrlen = 1000
gammashapemodel = 1000
uniqueswapbias = 0.1000
distanceswapbias = 1

bootstrapreps =
inferinternalstateprobs = 0

No partitions, with additional outgroups:

```
[general]
datafname = NoPart_withOG_ML.nex
constraintfile =
streefname = random
ofprefix = NoPart_withOG
randseed = -1
availablememory = 1000
logevery = 50
saveevery = 100
refinestart = 1
outputeachbettertopology = 1
enforcetermconditions = 1
genthreshfortopoterm = 5000
scorethreshforterm = 0.0500
significanttopochange = 0.0010
outputphyliptree = 0
outputmostlyuselessfiles = 0
writecheckpoints = 0
restart = 0
searchreps = 20


datatype=standard
ratematrix = 1rate
statefrequencies = equal
ratehetmodel = none
numratecats = 1
invariantsites = none



[master]
nindivs = 4
holdover = 1
selectionintensity = 0.5000
holdoverpenalty = 0
stopgen = 2147483646
stoptime = 2147483646

startoptprec = 0.5000
minoptprec = 0.0100
numberofprecreductions = 20
```

treerejectionthreshold = 50.0
topoweight = 1
modweight = 0.0500
brlenweight = 0.2000
randnniweight = 0.1000
randsprweight = 0.3000
limsprweight = 0.6000
intervallength = 100
intervalstostore = 5

limsprrange = 6
meanbrlenmuts = 5
gammashapebrlen = 1000
gammashapemodel = 1000
uniqueswapbias = 0.1000
distanceswapbias = 1

bootstrapreps =
inferinternalstateprobs = 0

Stepping-Stone

159 Characters with additional outgroups, outgroup constraint, partitioned, branch lengths unlinked

begin mrbayes;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245;
	charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158 159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212 213 214 216 217 218 219 220;
	partition byanatomy = 2: skull, shell;
	set autoclose=no nowarn=yes;
	set partition=byanatomy;

```
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all);
        prset applyto=(all) ratepr=variable;
        constraint outgroup -1 = 1 39 40;
        prset topologypr = constraint (outgroup);
        mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
        mcmc;
        sumt;
        sump;
end;

begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all);
        prset applyto=(all) ratepr=variable;
        constraint outgroup -1 = 1 39 40;
        prset topologypr = constraint (outgroup);
        ss ngen=2000000;
        sumss;
end;
```

Outgroups added, no outgroup constraint, no partitions

```
begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
```

```
	charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
	set autoclose=no nowarn=yes;
	lset applyto=(all) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) topology=(all);
	prset applyto=(all) ratepr=variable;
	mcmc ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
end;

begin mrbayes;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
	charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
	set autoclose=no nowarn=yes;
	lset applyto=(all) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) topology=(all);
	prset applyto=(all) ratepr=variable;
	ss ngen=2000000;
	sumss;
end;
```

Outgroups added, outgroup constraint, no partitions

```
begin mrbayes;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
	set autoclose=no nowarn=yes;
	lset applyto=(all) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
```

```
        prset applyto=(all) ratepr=variable;
        constraint outgroup -1 = 1 39 40;
        prset topologypr = constraint (outgroup);
        mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
        nchains=4 savebrlens=yes;
        mcmc;
        sumt;
        sump;
end;

begin mrbayes;
        set autoclose=yes nowarn=yes;
        lset applyto=(1) coding=all rates=invgamma;
        constraint outgroup -1 = 1 39 40;
        prset topologypr = constraint (outgroup);
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
        prset applyto=(all) ratepr=variable;
        ss ngen=1500000;
        sumss;
end;
```

Partitions, branch lengths unlinked, no outgroup constraint

```
begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all);
        prset applyto=(all) ratepr=variable;
        prset applyto=(all) brlenspr=unconstrained:exponential(10.0);
```

```
	mcmc ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
end;

begin mrbayes;
	log start filename=BrLUL_NoOGCon.txt append;
	charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
	partition byanatomy = 2: skull, shell;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;

	set autoclose=no nowarn=yes;
	set partition=byanatomy;

	lset applyto=(all) rates=invgamma;

	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all);

	prset applyto=(all) ratepr=variable;

	ss ngen=1500000;

	sumss;

	log stop;

end;
```

Partitions, topology unlinked, outgroup constraint

```
begin mrbayes;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
	charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
```

```
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) topology=(all);
        prset applyto=(all) ratepr=variable;
        constraint outgroup -1 = 1 39 40;
        prset topologypr = constraint (outgroup);
        mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
        mcmc;
        sumt;
        sump;
end;

begin mrbayes;

log start filename=Part_OGAdded_OGCon_TopoUL.txt append;

exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;

        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) topology=(all);
        prset applyto=(all) ratepr=variable;
```

```
        constraint outgroup -1 = 1 39 40;
        prset topologypr = constraint (outgroup);
        ss ngen=1500000;
        sumss;
log stop;

end;
```

Partitions, all linked, no outgroup constraint

```
begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
        prset applyto=(all) ratepr=variable;
        mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
        mcmc;
        sumt;
        sump;
end;

begin mrbayes;
log start filename=AllLink_NoOGCon_SS.txt append;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
```

```
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
        prset applyto=(all) ratepr=variable;
        ss ngen=1500000;
        sumss;
        log stop;
        end;
```

Partitions, all linked, outgroup constraint

```
begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
        prset applyto=(all) ratepr=variable;
        constraint outgroup -1 = 1 39 40;
        prset topologypr = constraint (outgroup);
        mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
        mcmc;
        sumt;
        sump;
```

```
end;

begin mrbayes;

log start filename=Part_AllLinked_OGcon.txt append;
exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245;
	charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
	partition byanatomy = 2: skull, shell;

	set autoclose=no nowarn=yes;
	set partition=byanatomy;
	lset applyto=(1) rates=invgamma;
	lset applyto=(2) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
	prset applyto=(all) ratepr=variable;
	constraint outgroup -1 = 1 39 40;
	prset topologypr = constraint (outgroup);
	ss ngen=1500000;
	sumss;

	log stop;
end;
```

Partitions, topology unlinked, no outgroup constraint

```
begin mrbayes;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
	charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
```

```
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) topology=(all);
        prset applyto=(all) ratepr=variable;
        mcmc ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
end;

begin mrbayes;

log start filename=TopoUL_NoOGCon_SS.txt append;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;

        set autoclose=no nowarn=yes;
        set partition=byanatomy;

        lset rates=gamma;
        unlink shape=(all);

        prset ratepr=variable;

        ss ngen=1500000;
        sumss;

        log stop;
end;
```

Partitions, branch lengths and topology unlinked, no outgroup constraint

```
begin mrbayes;
```

```
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
	charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
	partition byanatomy = 2: skull, shell;
	set autoclose=no nowarn=yes;
	set partition=byanatomy;
	lset applyto=(1) rates=invgamma;
	lset applyto=(2) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all);
	prset applyto=(all) ratepr=variable;
	prset applyto=(all) brlenspr=unconstrained:exponential(10.0);
	constraint outgroup -1 = 1 39 40;
	mcmc ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
end;

begin mrbayes;
	log start filename=BrLUL_NoOGCon.txt append;
	charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
	partition byanatomy = 2: skull, shell;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;

	set autoclose=no nowarn=yes;
	set partition=byanatomy;

	lset applyto=(all) rates=invgamma;

	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all);
```

```
        prset applyto=(all) ratepr=variable;

        ss ngen=1500000;

        sumss;

        log stop;

end;
```

Partitions, branch lengths and topology unlinked, outgroup constraint

```
begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all) topology=(all);
        prset applyto=(all) ratepr=variable;
        constraint outgroup -1 = 1 39 40;
        prset topologypr = constraint (outgroup);
        mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
        mcmc;
        sumt;
        sump;
end;


begin mrbayes;
```

```
log start filename=Part_OGAdded_OGCon_BrLUL_TopoUL_SS.txt append;

exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245;
	charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
	partition byanatomy = 2: skull, shell;

	set autoclose=no nowarn=yes;
	set partition=byanatomy;
	lset applyto=(1) rates=invgamma;
	lset applyto=(2) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all) topology=(all);
	prset applyto=(all) ratepr=variable;
	constraint outgroup -1 = 1 39 40;
	prset topologypr = constraint (outgroup);
	ss ngen=1500000;
	sumss;
	log stop;
end;
```

Shell only, no outgroup constraint

```
begin mrbayes;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245
14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45
46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77
78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	set autoclose=no nowarn=yes;
	lset applyto=(all) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
	prset applyto=(all) ratepr=variable;
	mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
	mcmc;
	sumt;
	sump;
end;
```

Shell only, outgroup constraint

```
begin mrbayes;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245
14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45
46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77
78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	set autoclose=no nowarn=yes;
	lset applyto=(all) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
	prset applyto=(all) ratepr=variable;
	constraint outgroup -1 = 1 39 40;
	prset topologypr = constraint (outgroup);
	mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
	mcmc;
	sumt;
	sump;
end;
```

Skull only, no outgroup constraint

```
begin mrbayes;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245
81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158 159 160 161 162 163 164
165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 189 190 191 192 193 194
195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212 213 214 216 217 218 219
220;
	set autoclose=no nowarn=yes;
	lset applyto=(1) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
	prset applyto=(all) ratepr=variable;
	mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
	mcmc;
	sumt;
	sump;
end;
```

Skull only, outgroup constraint

```
begin mrbayes;
```

exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158 159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212 213 214 216 217 218 219 220;
set autoclose=no nowarn=yes;
lset applyto=(1) rates=invgamma;
unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
prset applyto=(all) ratepr=variable;
constraint outgroup -1 = 1 39 40;
prset topologypr = constraint (outgroup);
mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25 printfreq=1000 samplefreq=1000 nchains=4 savebrlens=yes;
mcmc;
sumt;
sump;
end;

No partitions, no outgroups added

begin mrbayes;
exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245;
set autoclose=no nowarn=yes;
lset applyto=(1) rates=invgamma;
unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all) topo=(all);
prset applyto=(all) ratepr=variable;
mcmc ngen= 20000000 relburnin=yes burninfrac=0.25 printfreq=1000 samplefreq=1000 nchains=4 savebrlens=yes;
end;

begin mrbayes;

log start filename=NoPart_DelOG_SS.txt append;
exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245;
charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158 159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182

```
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        set autoclose=no nowarn=yes;
        lset applyto=(all) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) topology=(all);
        prset applyto=(all) ratepr=variable;

        ss ngen=1500000;
        sumss;

        log stop;
end;
```

Partitions all linked, no outgroups added

```
begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
        prset applyto=(all) ratepr=variable;
        mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
        mcmc;
        sumt;
        sump;
end;

begin mrbayes;

log start filename=Part_AllLinked_DelOG.txt append;
```

```
exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;

        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
        prset applyto=(all) ratepr=variable;
        ss ngen=1500000;
        sumss;

        log stop;
end;
```

Partitions, branch lengths unlinked, no outgroups added

```
begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all);
        prset applyto=(all) ratepr=variable;
```

```
        mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
        mcmc;
        sumt;
        sump;
end;

begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all);
        prset applyto=(all) ratepr=variable;
        ss ngen=1500000;
        sumss;
end;
```

Partitions, topology unlinked, no additional outgroups

```
begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
```

```
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) topo=(all);
        prset applyto=(all) ratepr=variable;
        mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
        mcmc;
        sumt;
        sump;
end;

begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
        charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158
159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182
189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212
213 214 216 217 218 219 220;
        partition byanatomy = 2: skull, shell;
        set autoclose=no nowarn=yes;
        set partition=byanatomy;
        lset applyto=(1) rates=invgamma;
        lset applyto=(2) rates=invgamma;
        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all);
        prset applyto=(all) ratepr=variable;
        ss ngen=1500000;
        sumss;
end;
```

Partitions, branch lengths and topology unlinked, no additional outgroups

```
begin mrbayes;
        exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-
245;
        charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215
221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43
```

44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158 159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212 213 214 216 217 218 219 220;
partition byanatomy = 2: skull, shell;
set autoclose=no nowarn=yes;
set partition=byanatomy;
lset applyto=(1) rates=invgamma;
lset applyto=(2) rates=invgamma;
unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all) topo=(all);
prset applyto=(all) ratepr=variable;
mcmc ngen= 20000000 relburnin=yes burninfrac=0.25 printfreq=1000 samplefreq=1000 nchains=4 savebrlens=yes;
end;

begin mrbayes;

log start filename=Part_BrLUL_TopoUL_DelOG.txt append;
exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245;
charset skull = 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
charset shell = 81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158 159 160 161 162 163 164 165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212 213 214 216 217 218 219 220;
partition byanatomy = 2: skull, shell;

set autoclose=no nowarn=yes;
set partition=byanatomy;
lset applyto=(1) rates=invgamma;
lset applyto=(2) rates=invgamma;
unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) brlens=(all) topo=(all);
prset applyto=(all) ratepr=variable;

ss ngen=1500000;
sumss;

log stop;

```
end;
```

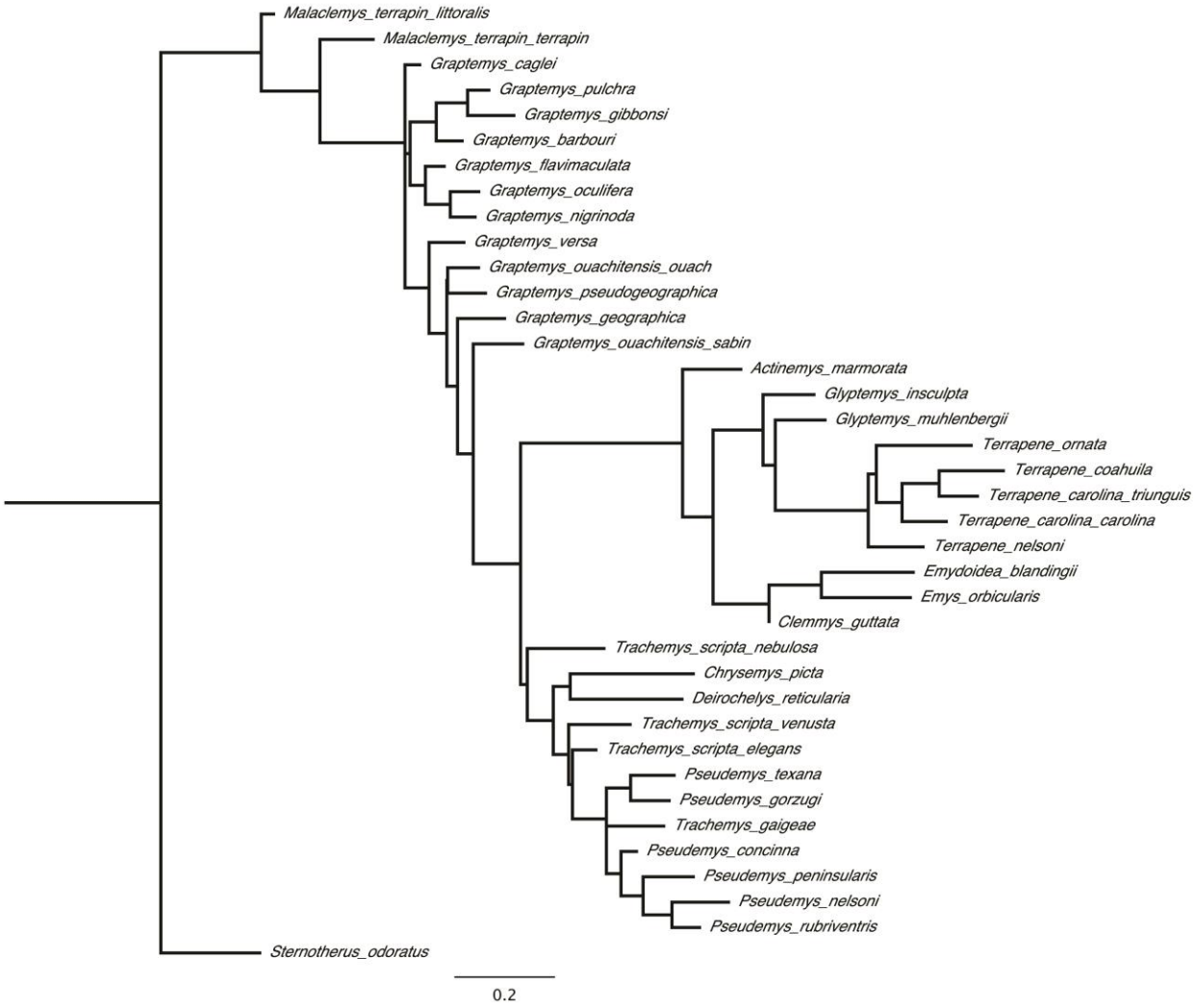
Skull only, no additional outgroups

```
begin mrbayes;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245
81 82 83 90 92 94 96 98 99 100 101 102 104 117 118 119 120 156 157 158 159 160 161 162 163 164
165 166 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 189 190 191 192 193 194
195 196 197 198 199 200 201 202 203 204 205 206 207 208 210 211 212 213 214 216 217 218 219
220;
	set autoclose=no nowarn=yes;
	lset applyto=(1) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
	prset applyto=(all) ratepr=variable;
	mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
	mcmc;
	sumt;
	sump;
end;
```

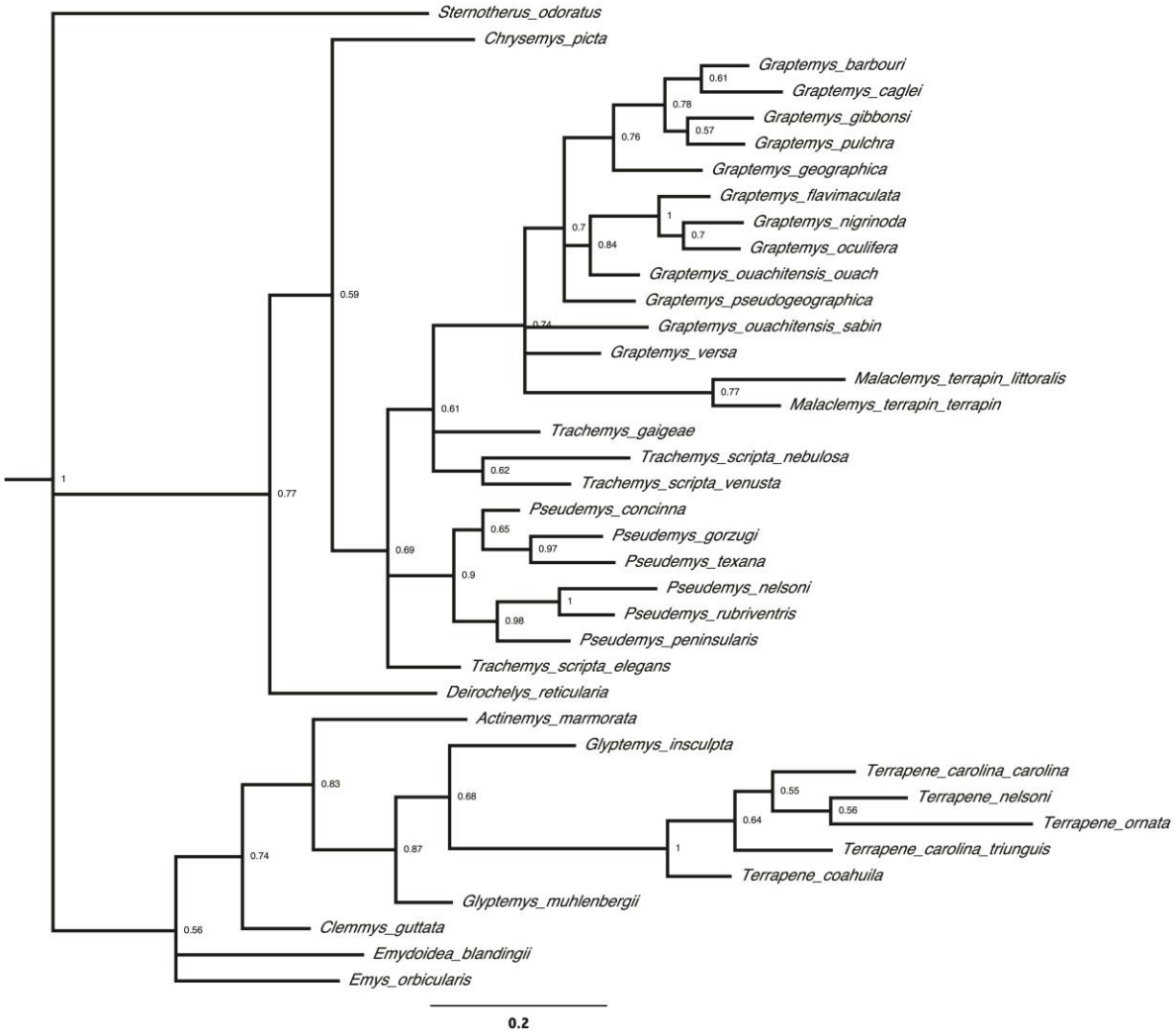
Shell only, no additional outgroups

```
begin mrbayes;
	exclude 1-13 84-89 91 93 95 97 103 105-116 121-134 142 143 167 183-188 209 215 221-245
14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45
46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77
78 79 80 135 136 137 138 139 140 141 144 145 146 147 148 149 150 151 152 153 154 155;
	set autoclose=no nowarn=yes;
	lset applyto=(all) rates=invgamma;
	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
	prset applyto=(all) ratepr=variable;
	mcmcp ngen= 20000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000
nchains=4 savebrlens=yes;
	mcmc;
	sumt;
	sump;
end;
```

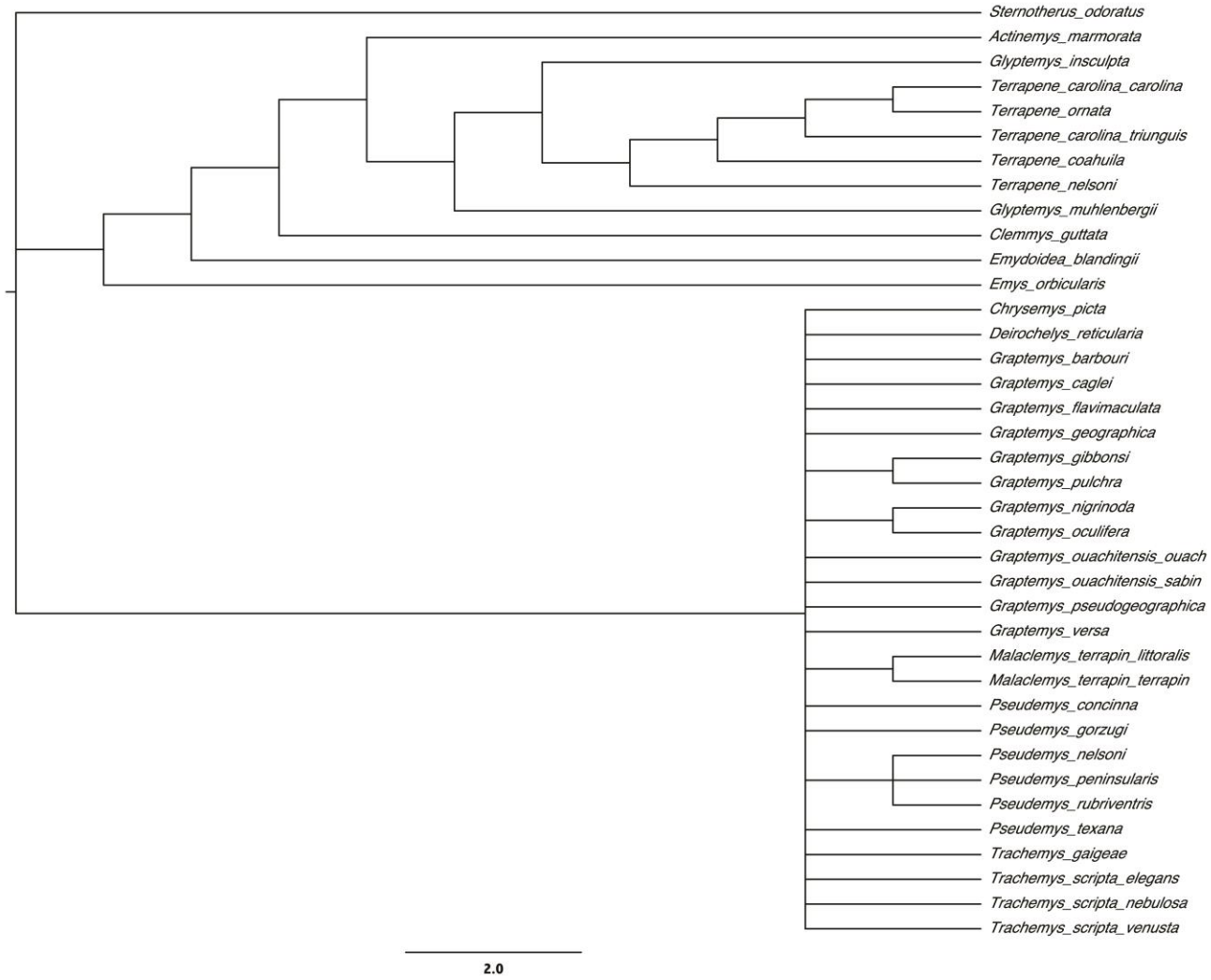
APPENDIX 7: TREES FROM RECONSTRUCTED PHYLOGENIES



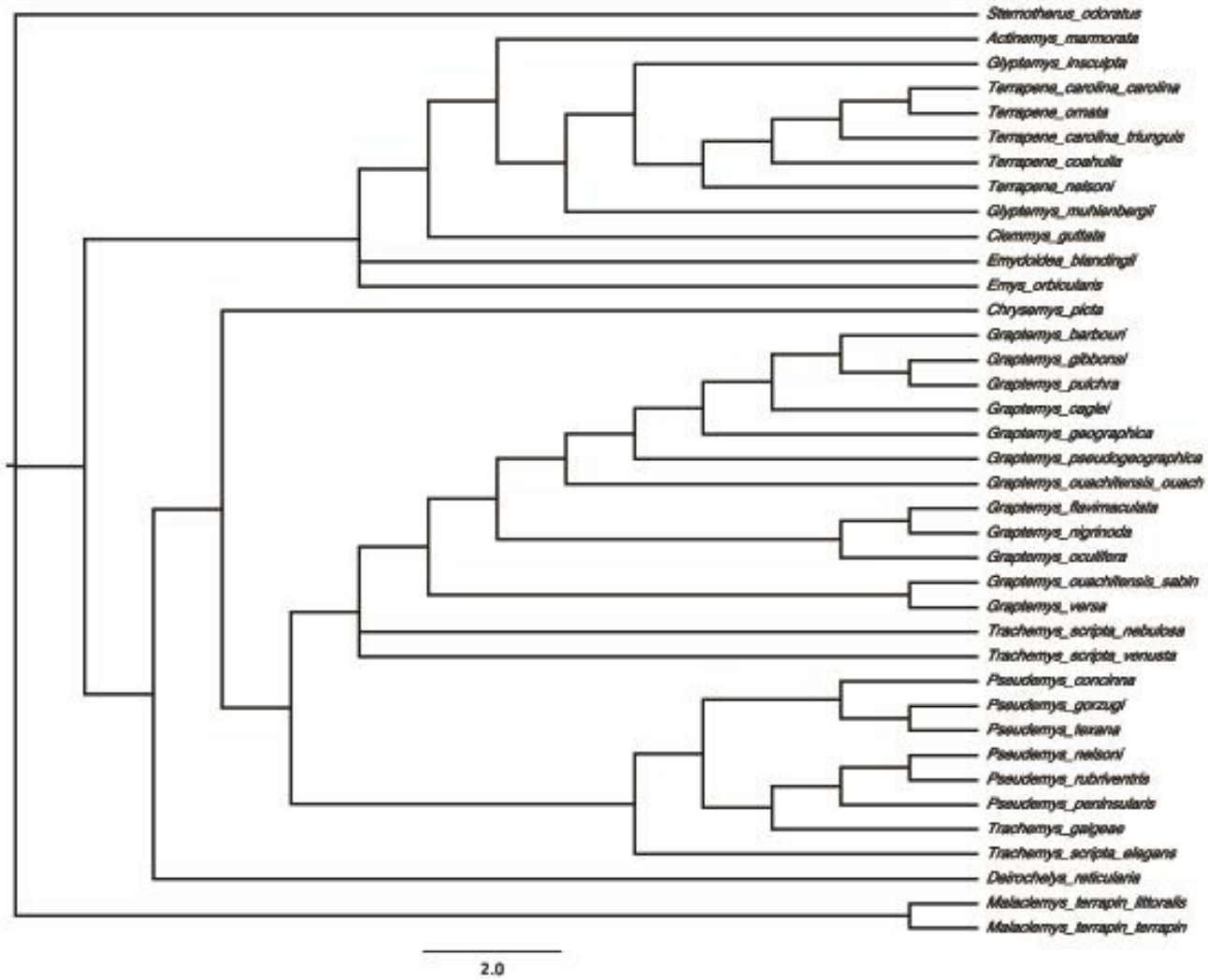
Maximum likelihood comparison tree, derived from all 245 morphological characters. Log likelihood -3358.38.



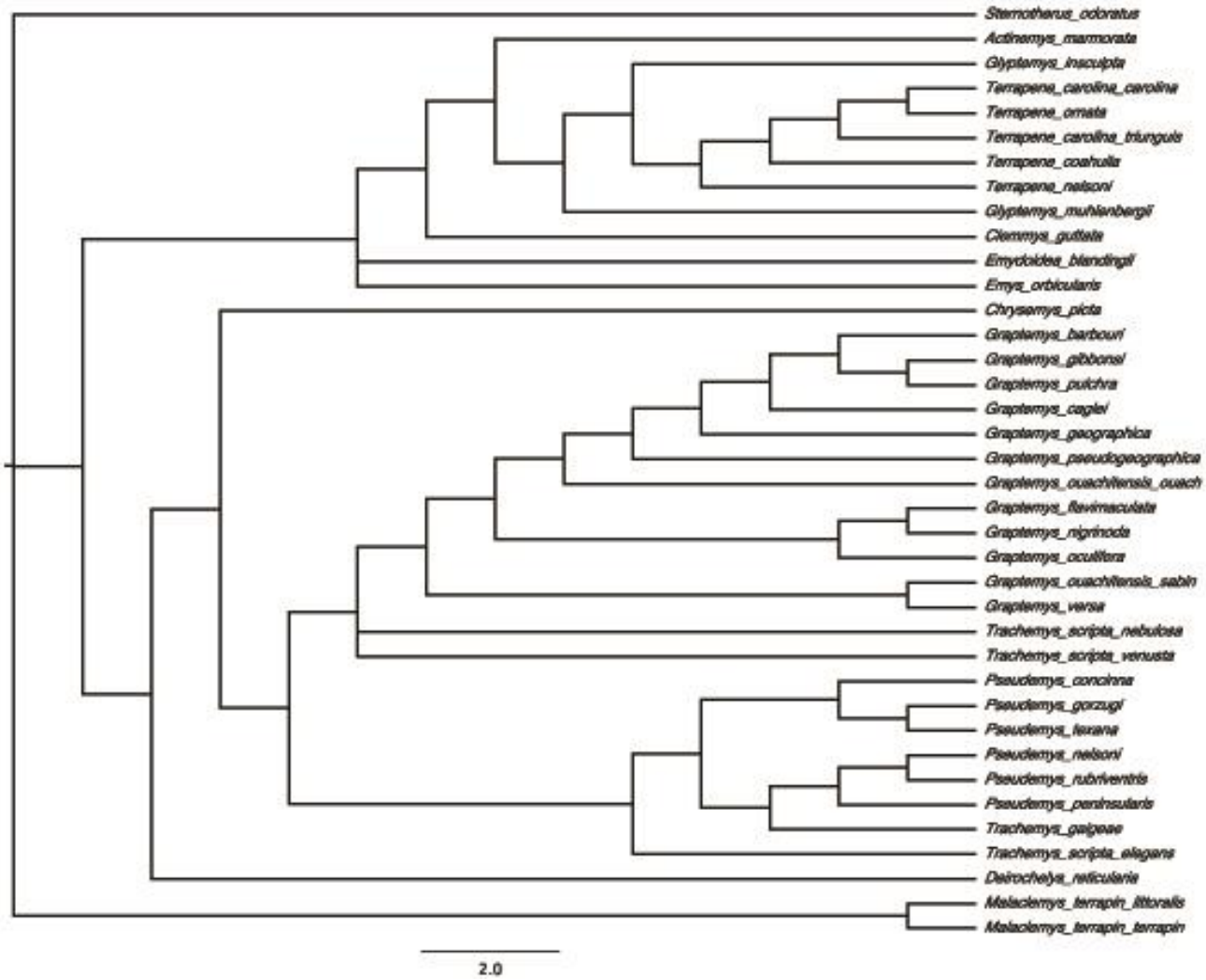
Bayesian comparison tree, constructed from all 245 morphological characters. .



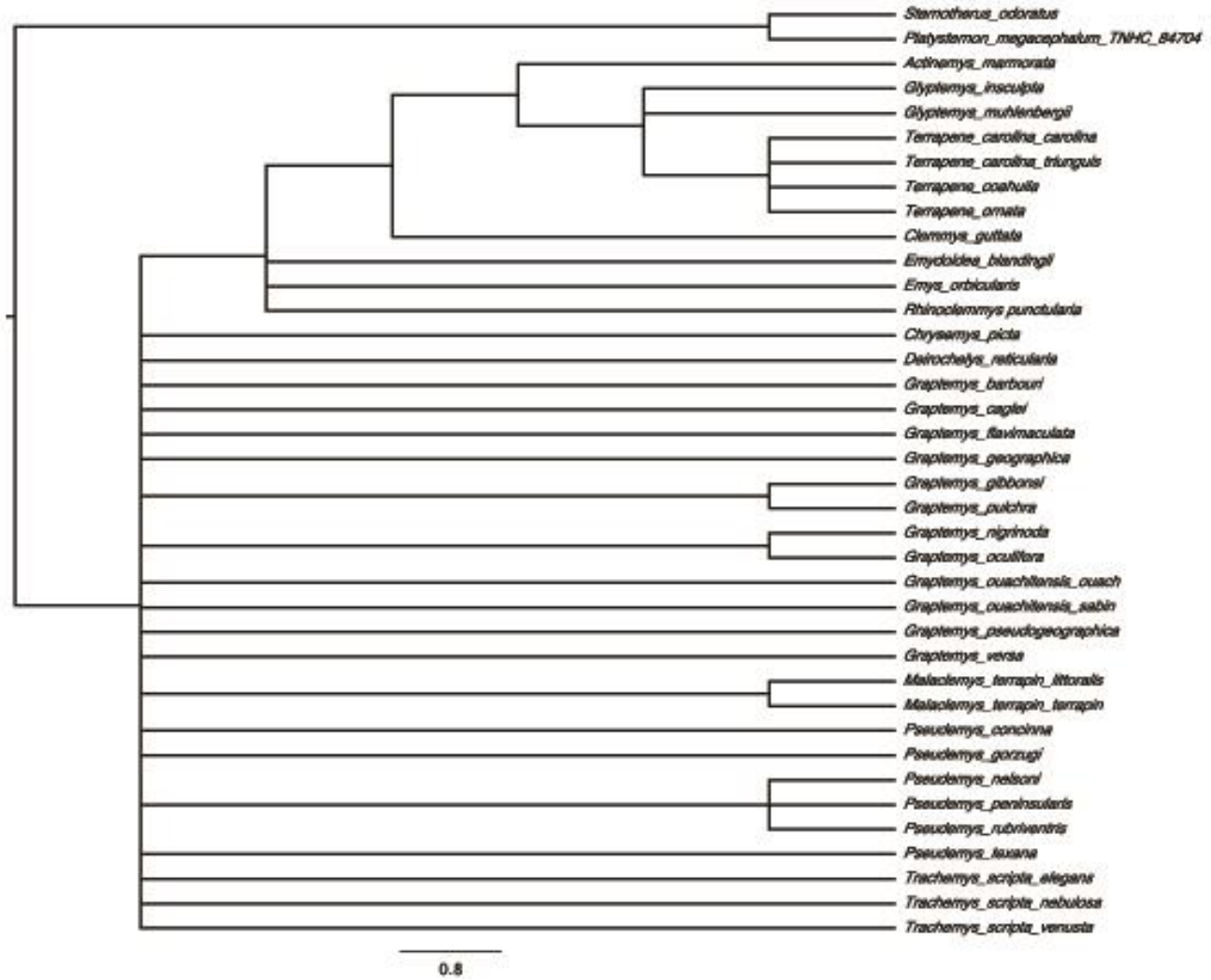
Strict consensus of 159-characters, with no additional outgroups, tree length 344-steps, 180 most parsimonious trees. .



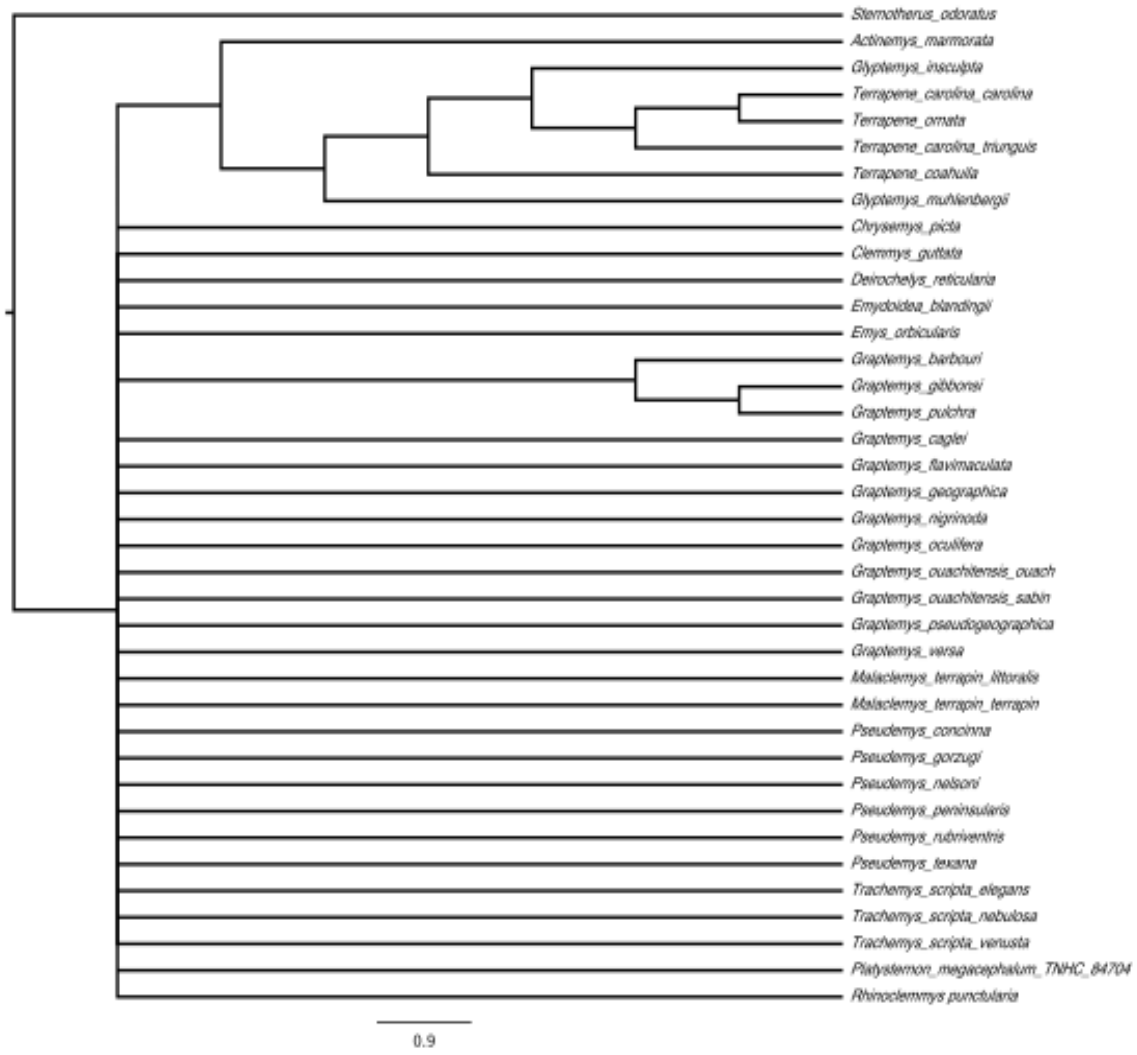
Parsimony utilizing only shell characters, with no additional outgroups, strict consensus of 4 most parsimonious trees with length 354 steps. .



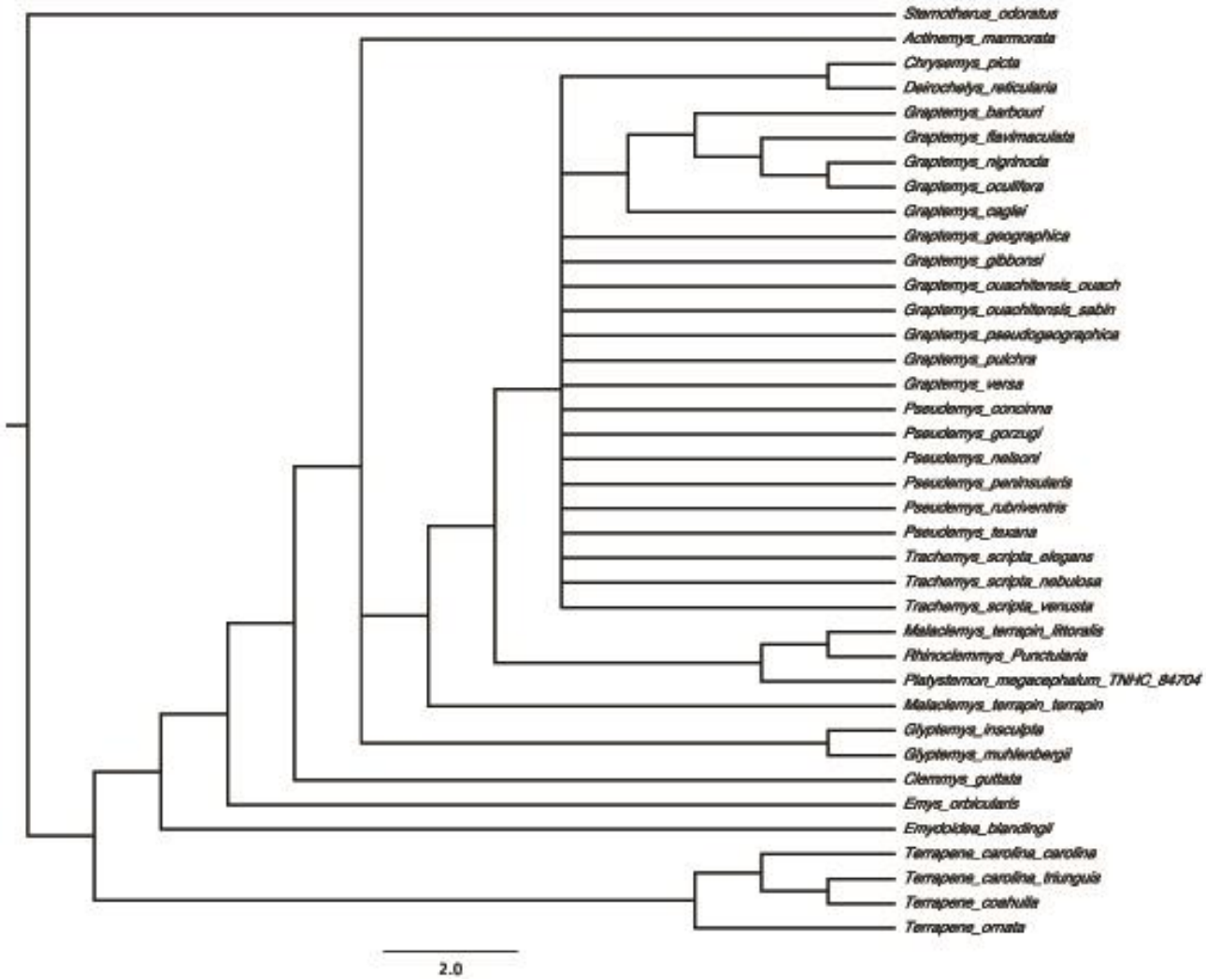
Parsimony strict consensus tree of 4 most parsimonious trees with length 300 steps, utilizing only head characters, with no additional outgroups. .



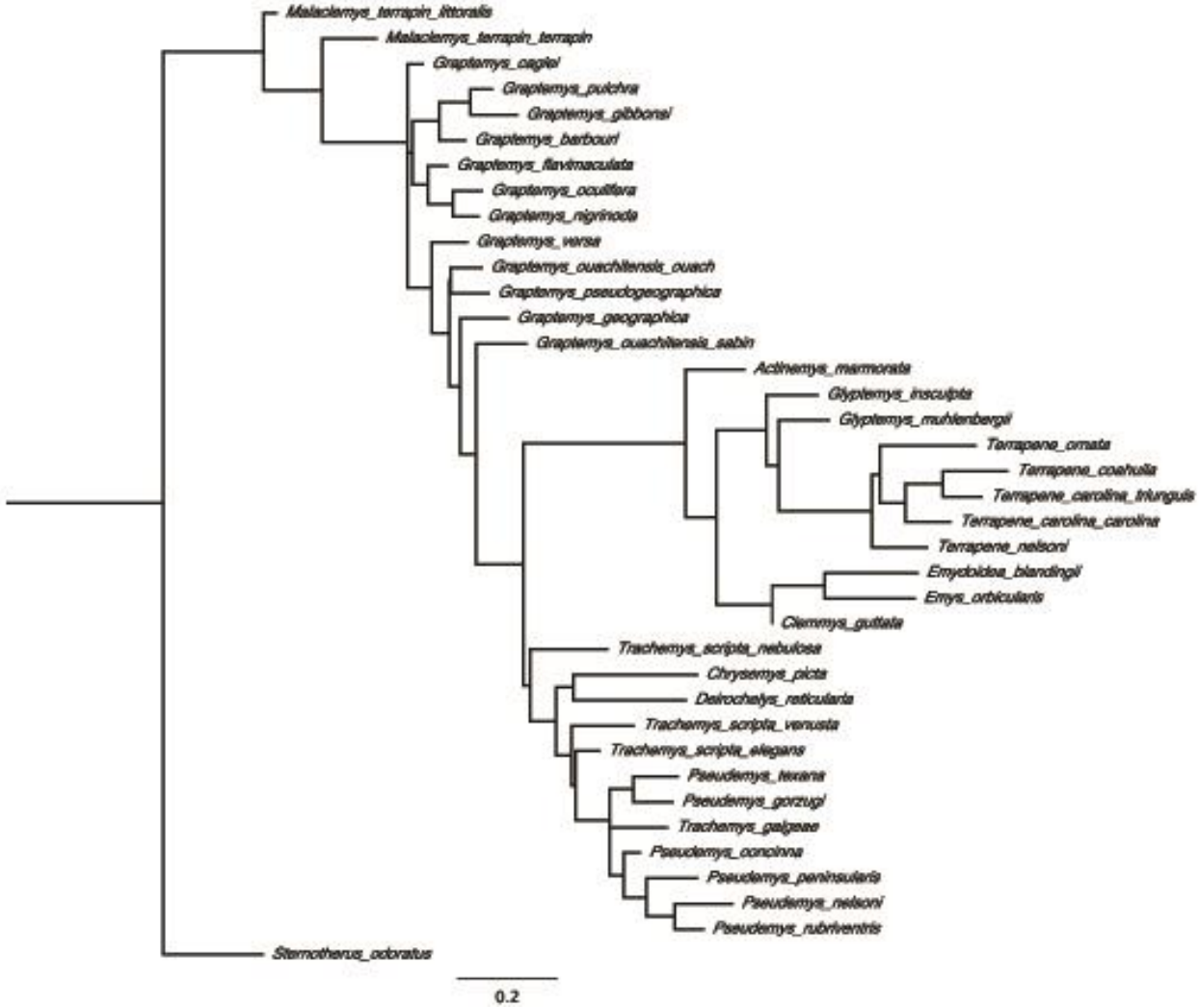
Strict consensus parsimony tree of 1171 most parsimonious trees with length 950 steps. 159-character matrix with additional outgroups. *Terrapene nelsoni* and *Trachemys gaigeae* were removed as taxonomic equivalents.



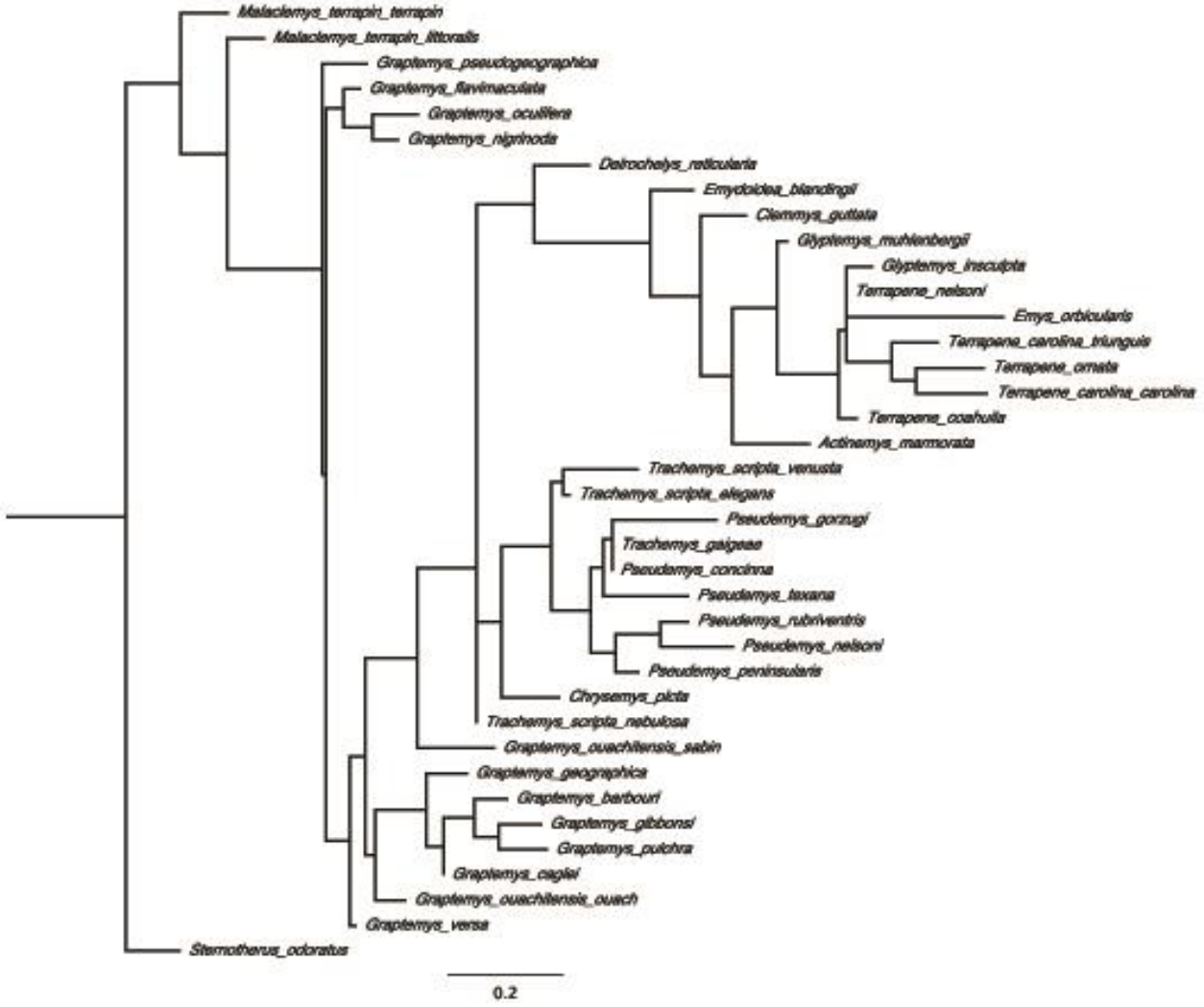
Parsimony strict consensus of 7941 most parsimonious trees with length 999 steps, from only head characters with additional outgroups and *Terrapene nelsoni* and *Trachemys gaigeae* removed.



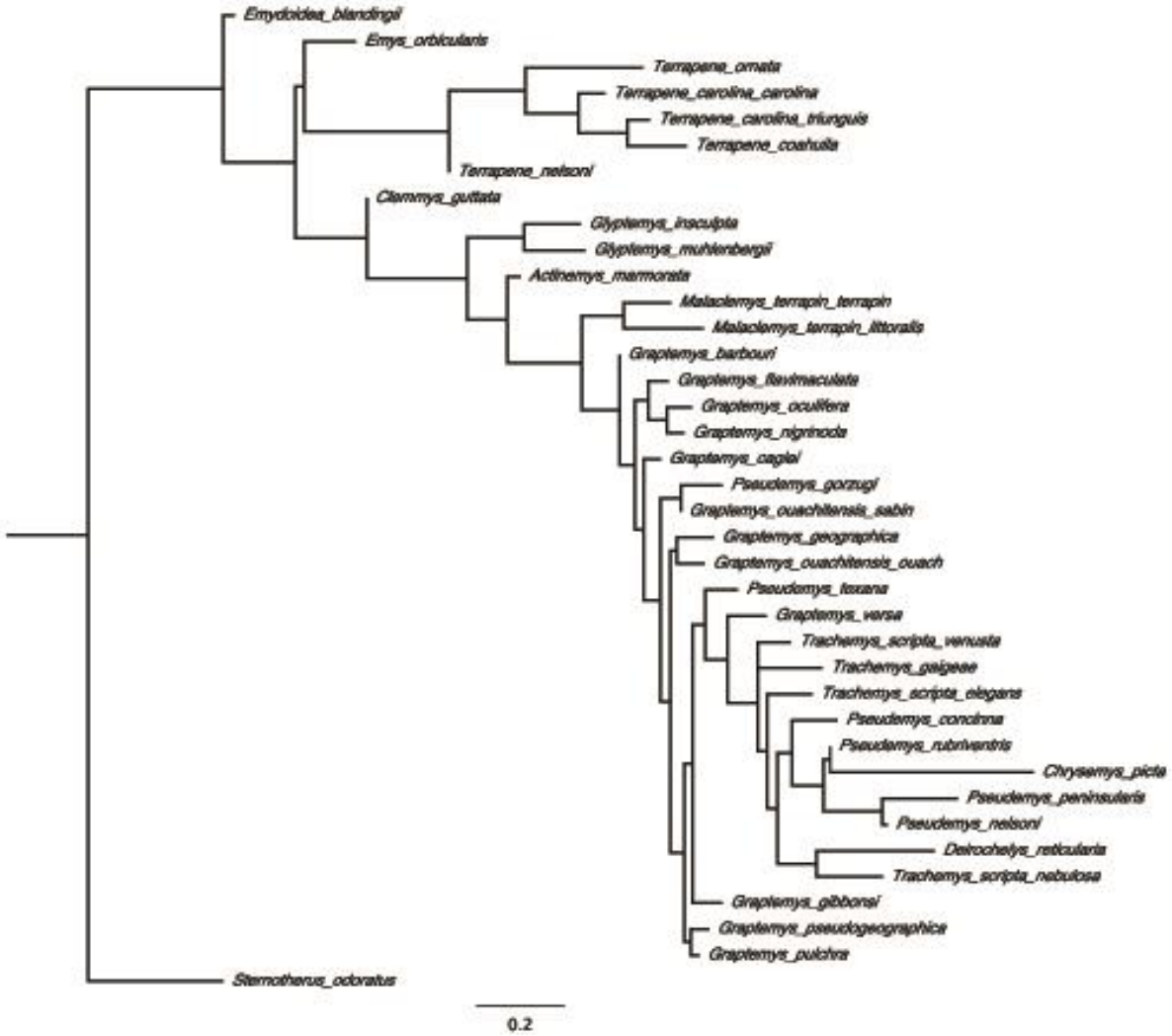
Strict consensus parsimony tree of 207 most parsimonious trees with length 1008 steps, utilizing only shell characters, with additional outgroups, and taxonomic equivalents *Terrapene nelsoni* and *Trachemys gaigeae* removed. .



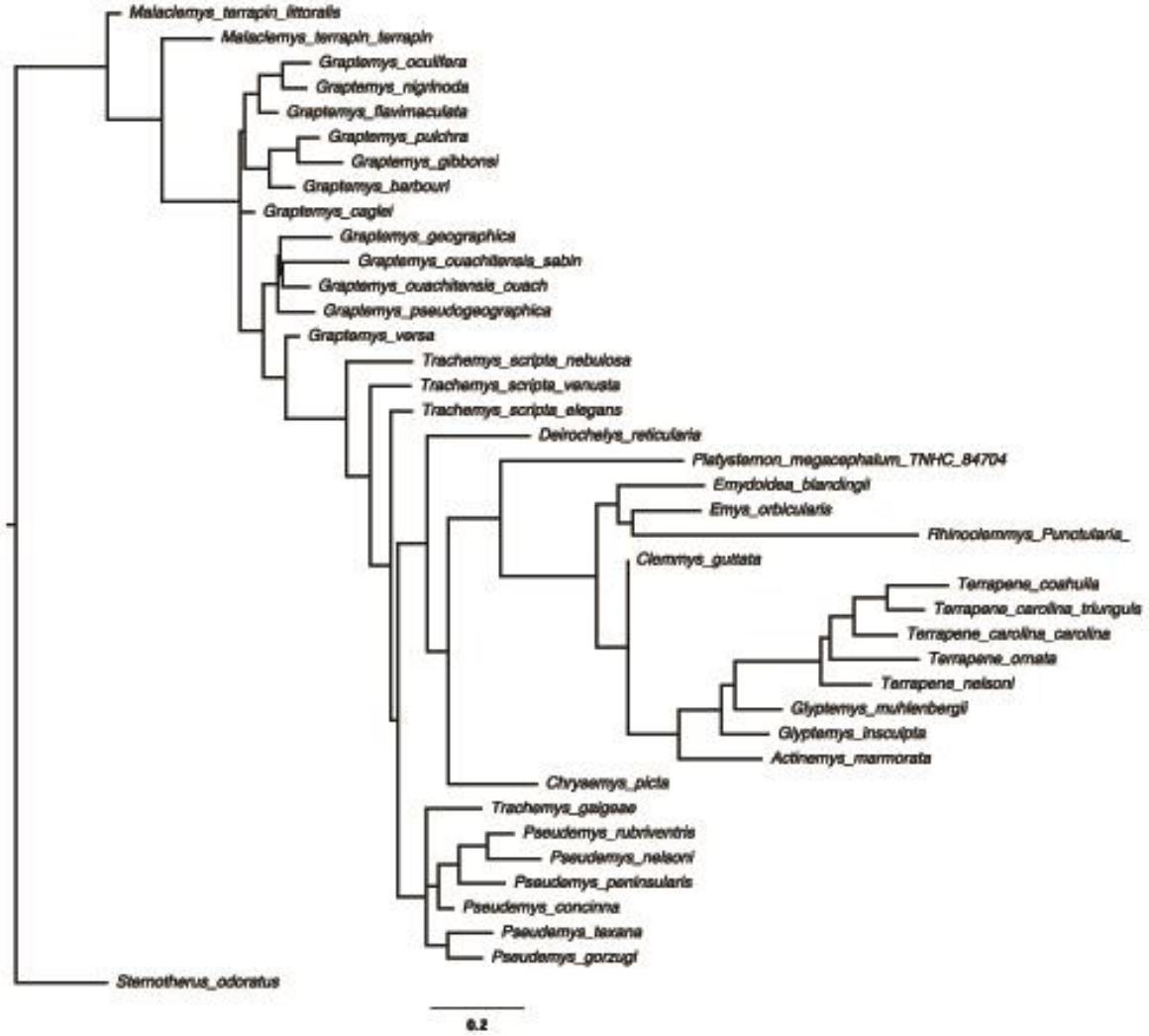
Maximum likelihood of 159-character matrix with no additional outgroups. Log likelihood of -2372.84.



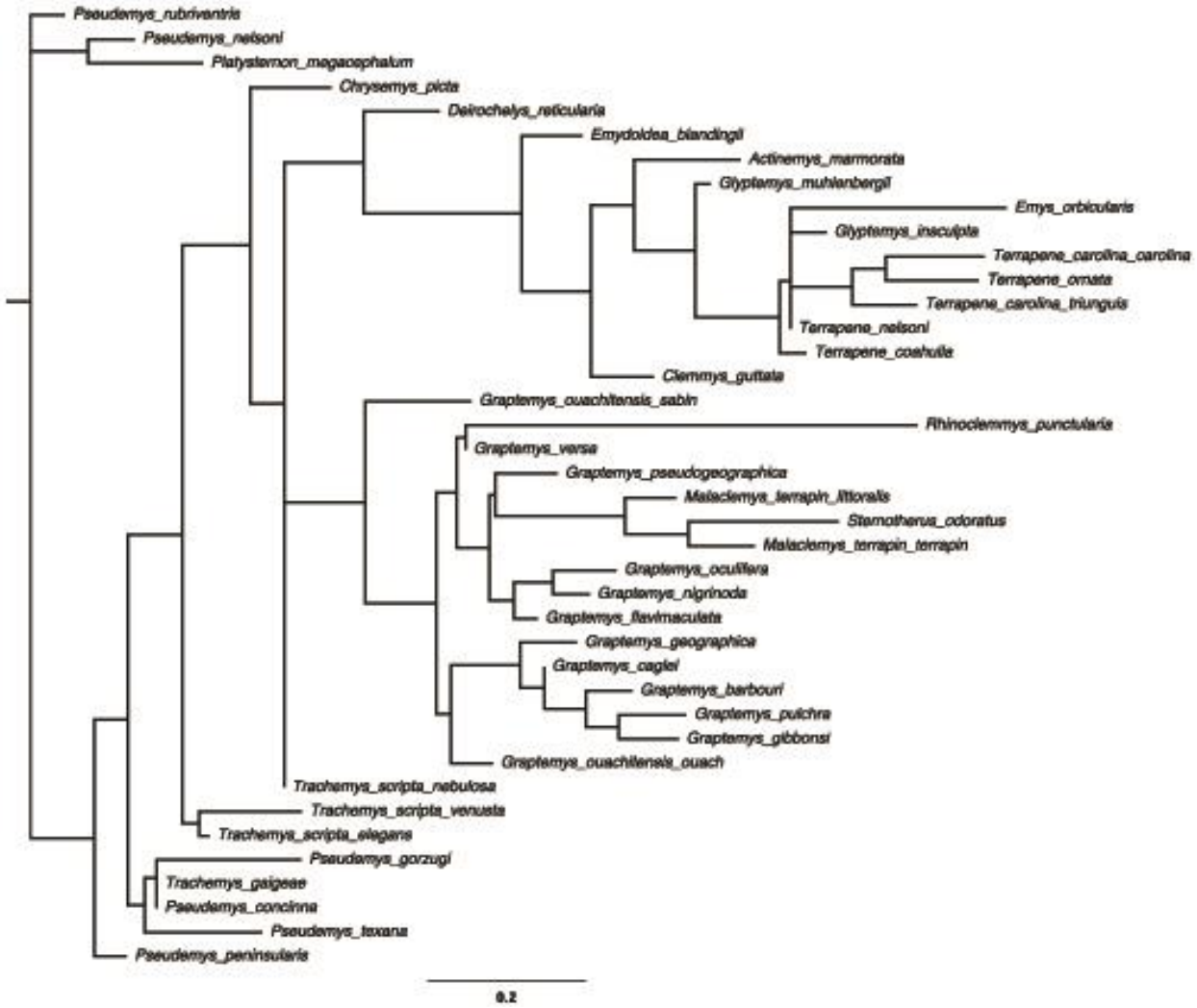
Maximum likelihood of only head characters with no additional outgroups. Log likelihood of -1077.64.



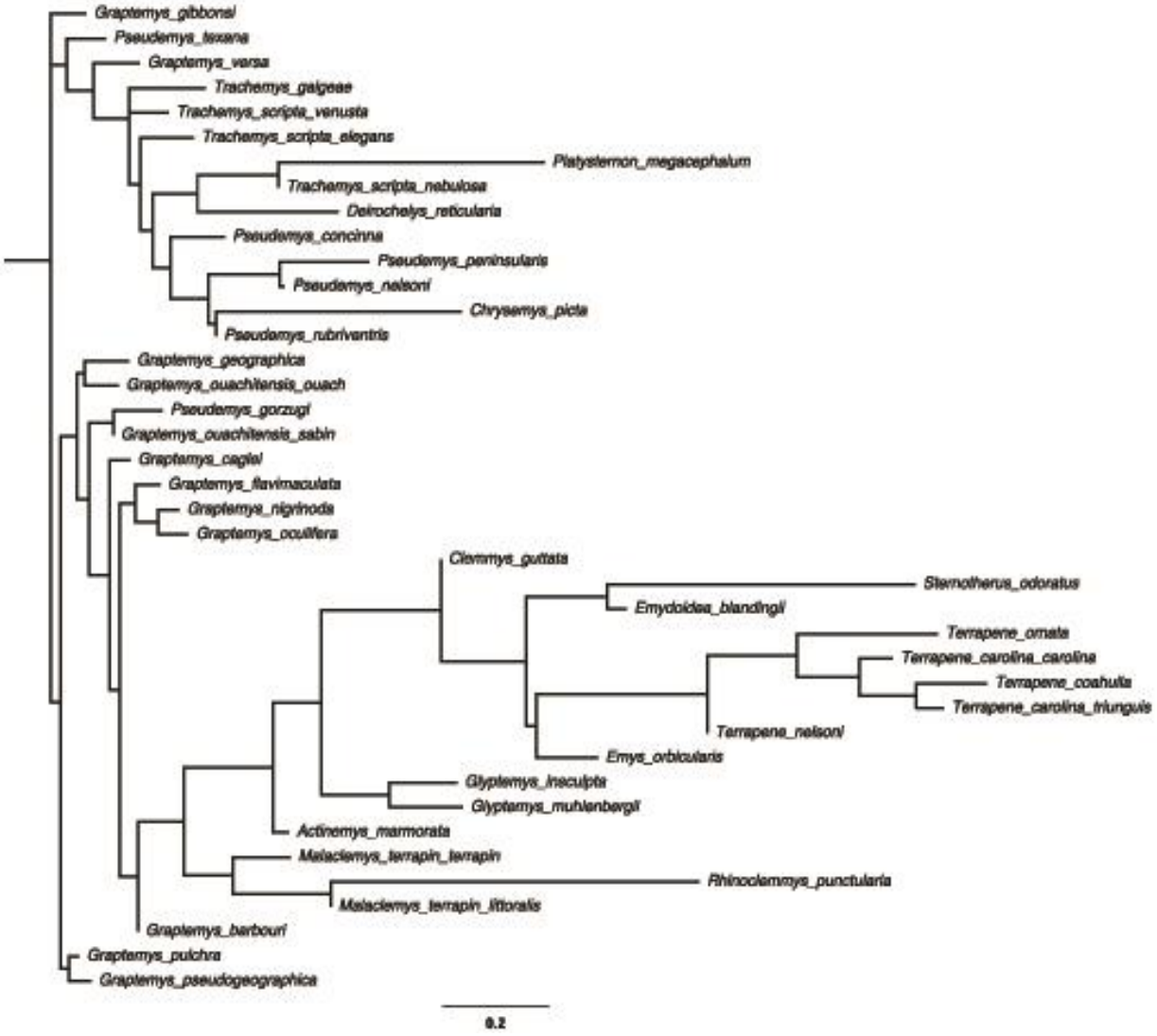
Maximum likelihood tree of only shell characters with no additional outgroups. Log likelihood value of -1177.81. .



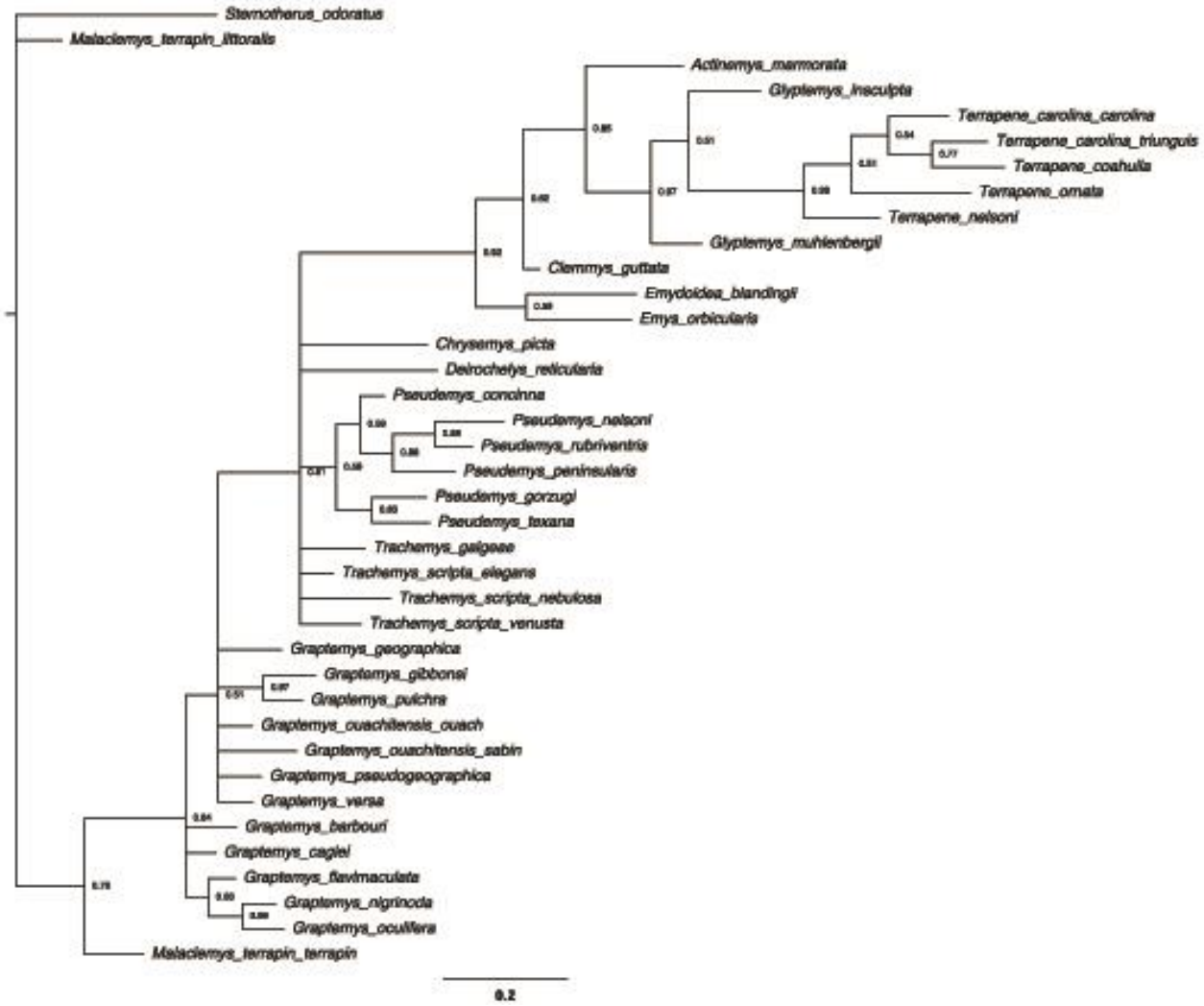
Maximum likelihood of 159-characters with additional outgroups. Log likelihood value of -2504.11.



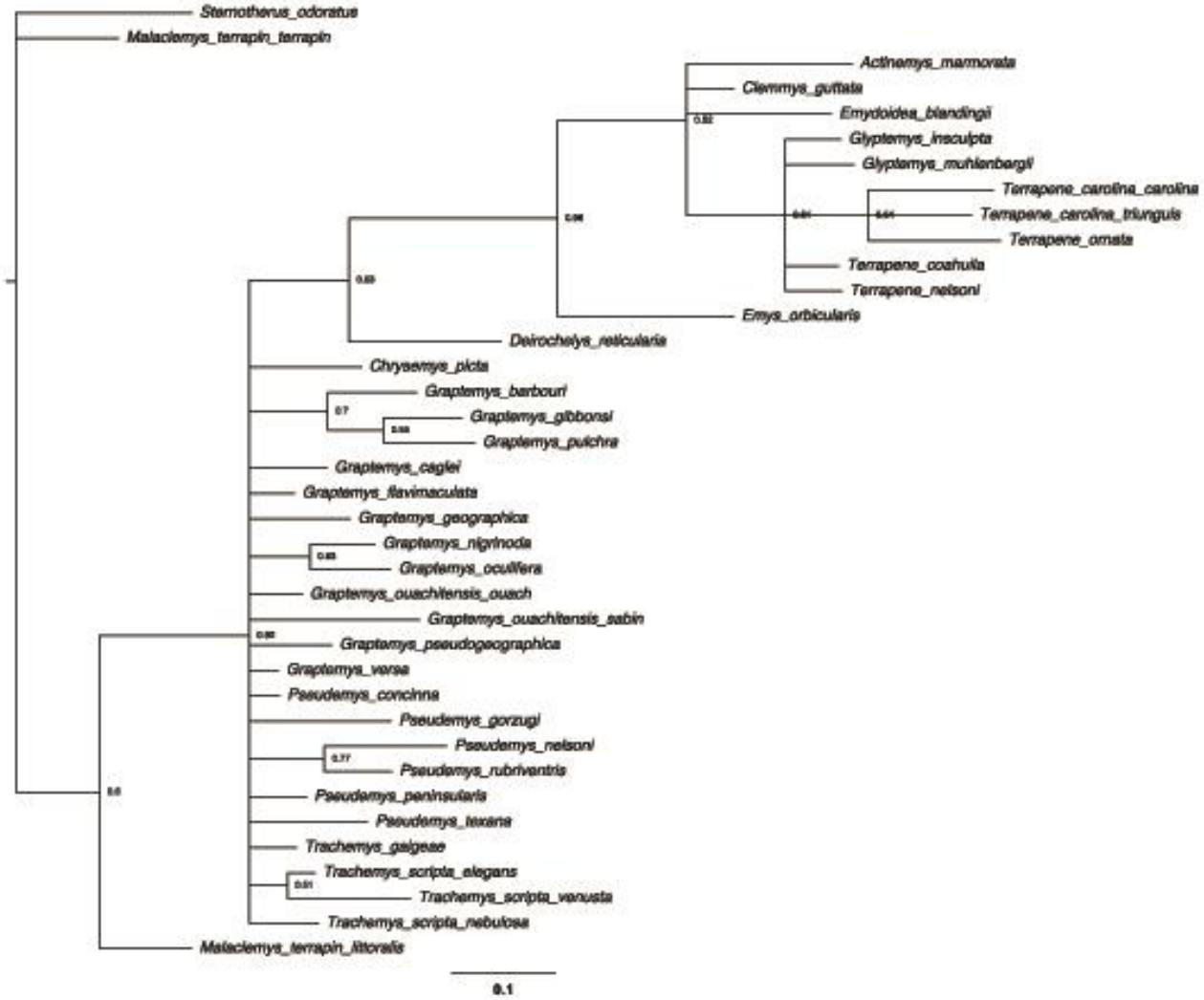
Maximum likelihood of head characters with additional outgroups. Log likelihood value of -1123.25.



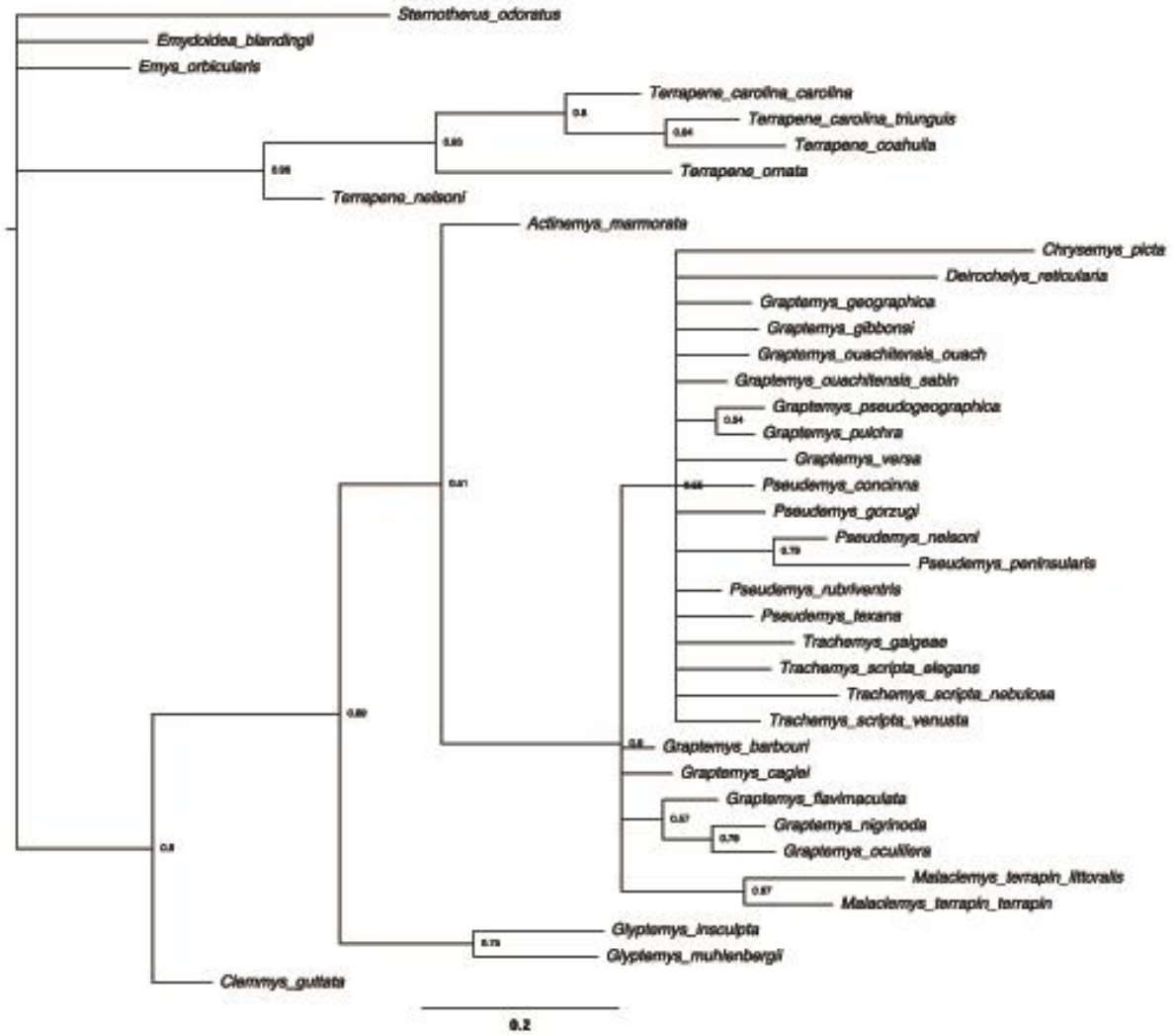
Maximum likelihood of only shell characters with additional outgroups. Log likelihood value of -1259.06.



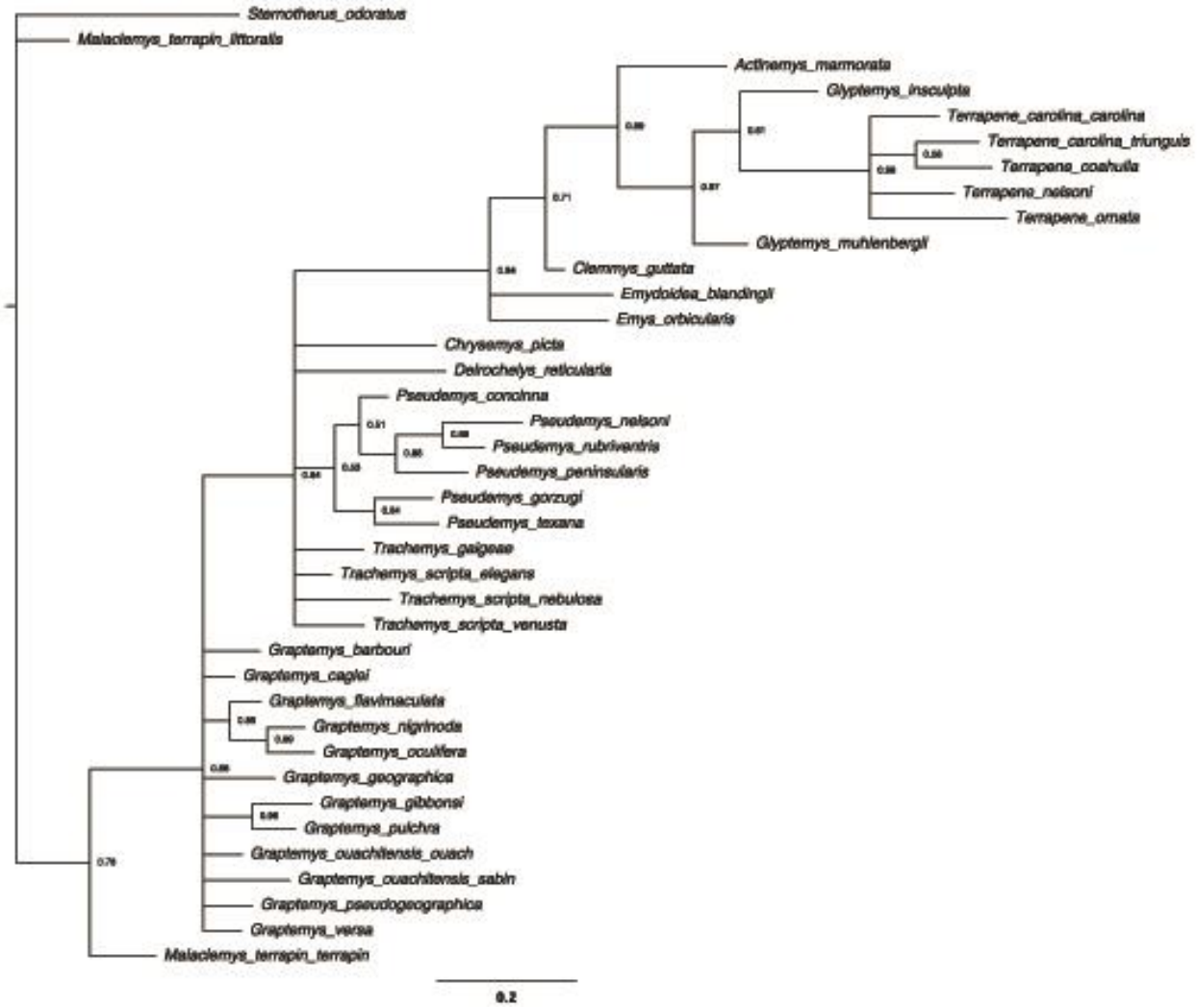
Bayesian tree of 159-character matrix, with no partitions and no additional outgroups.



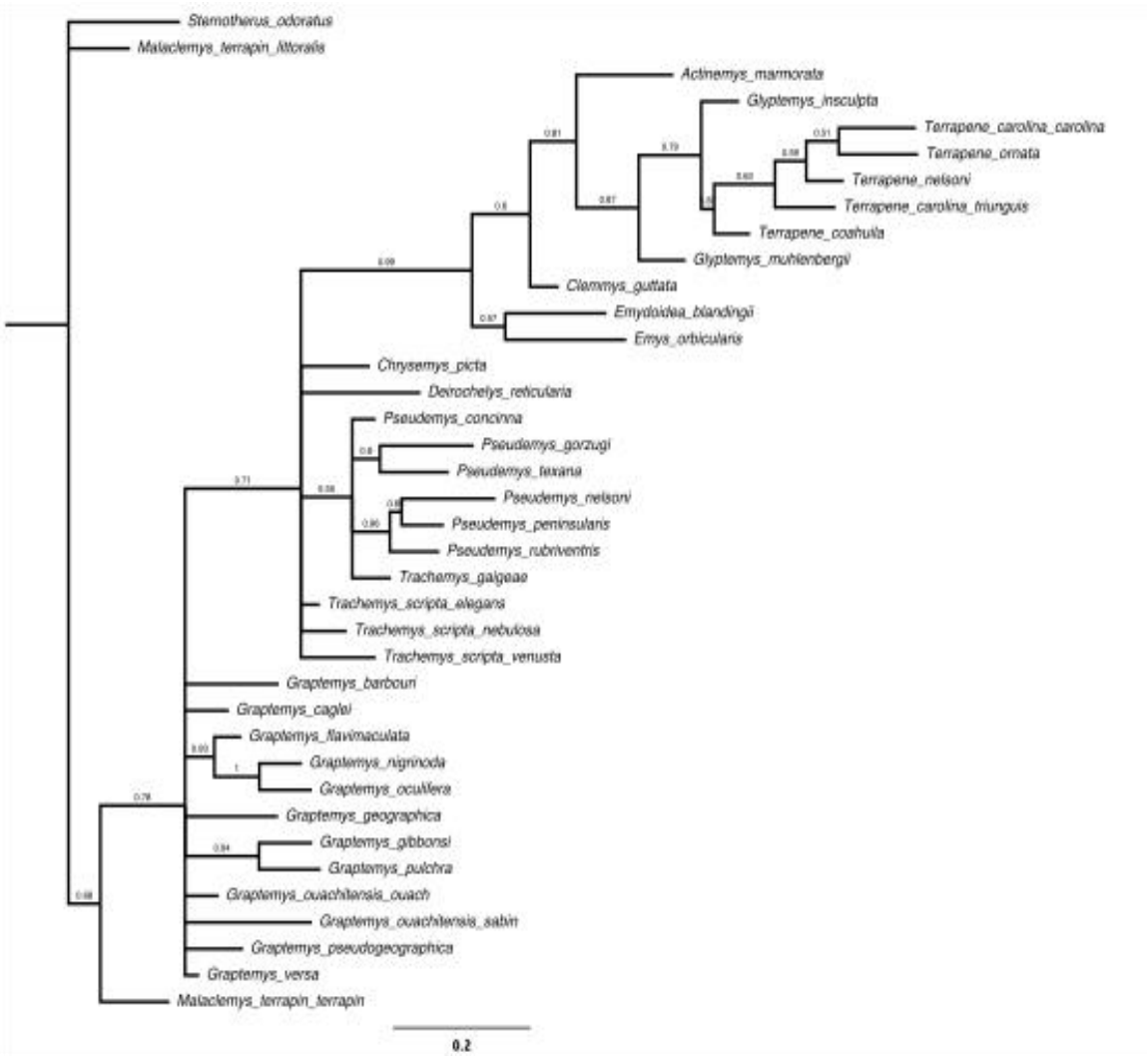
Bayesian analysis of only head characters with no additional outgroups.



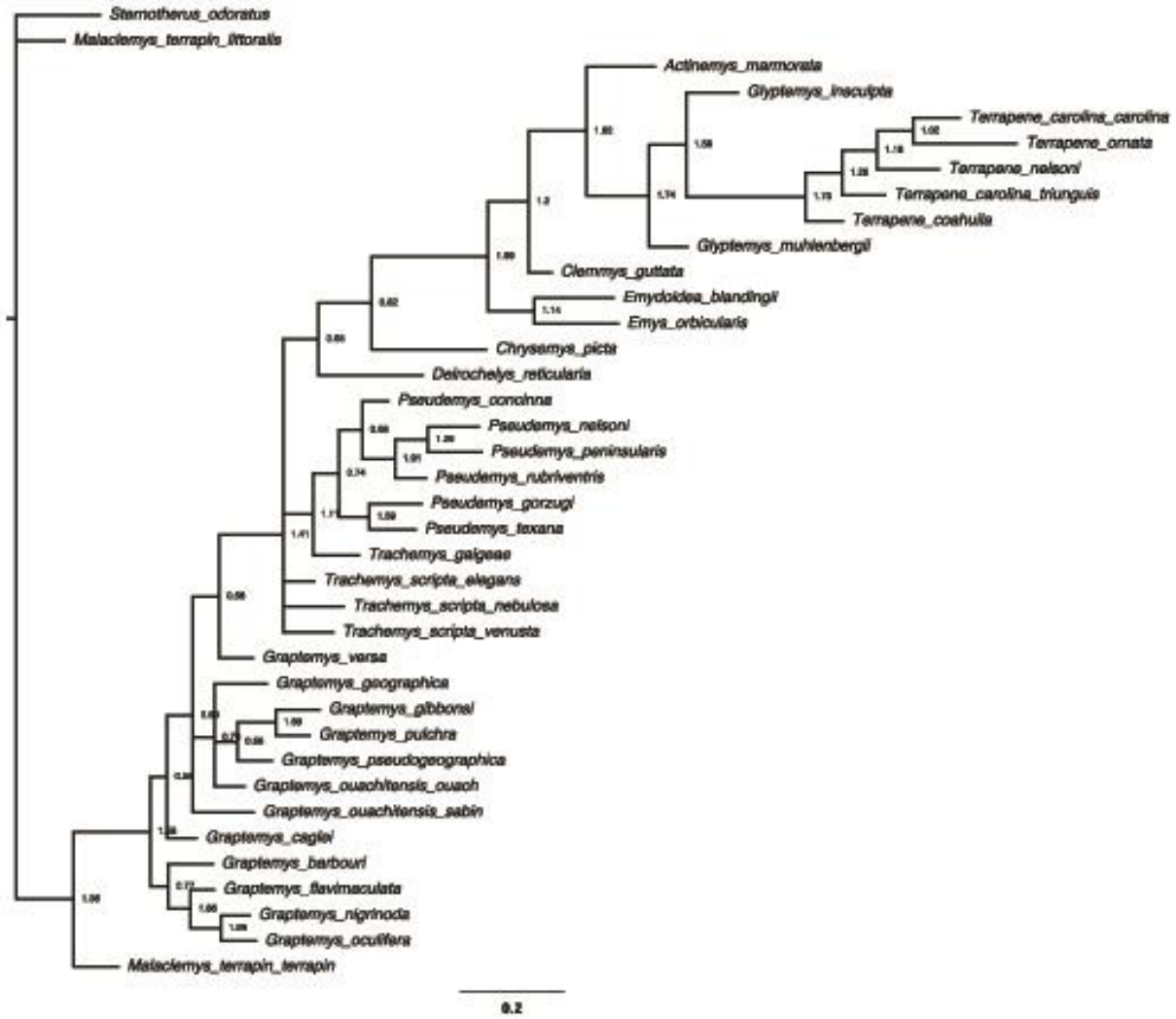
Bayesian analysis of only shell characters with no additional outgroups. .



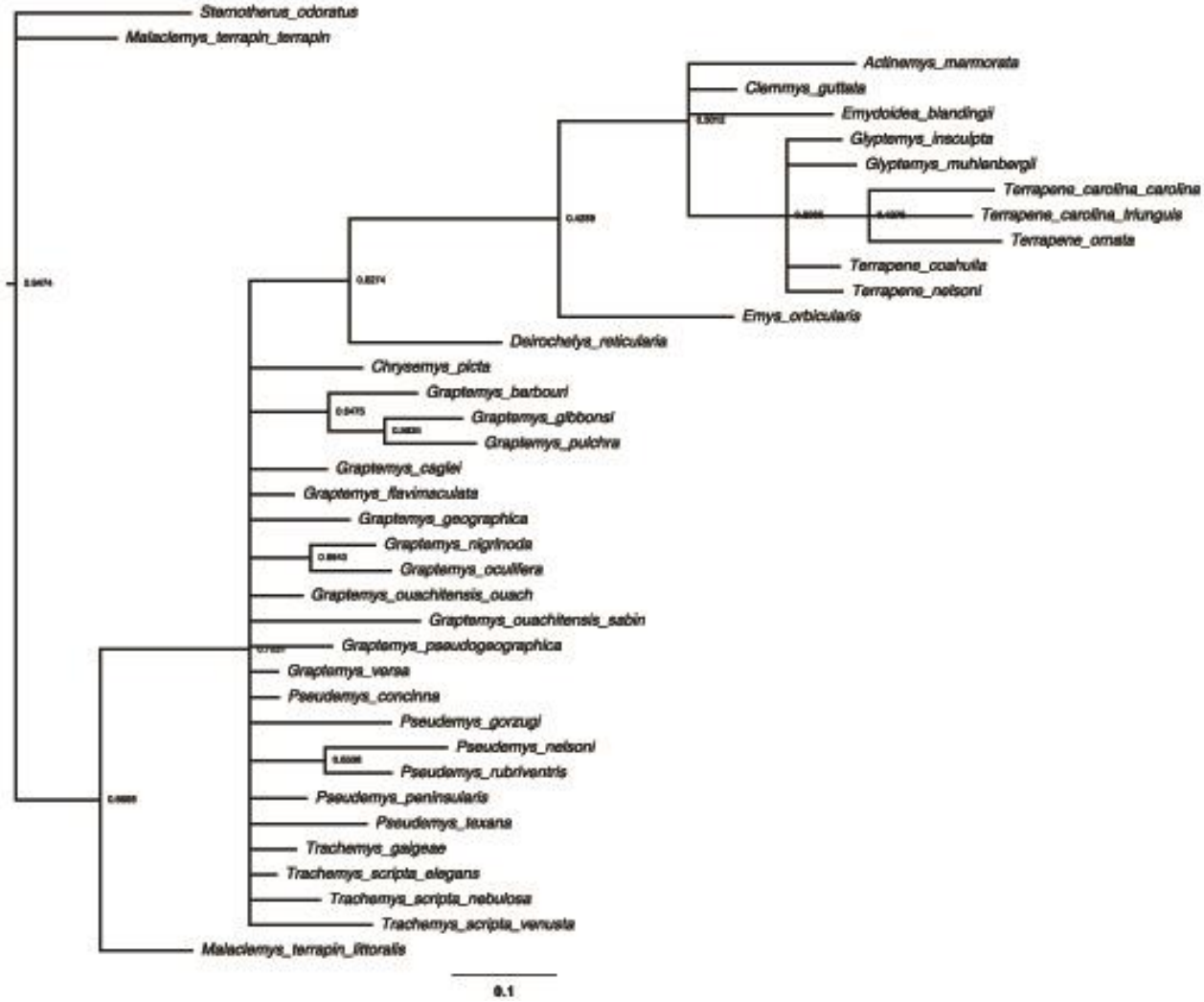
Bayesian analysis with each anatomical region partitioned, with all parameters linked, with no additional outgroups.



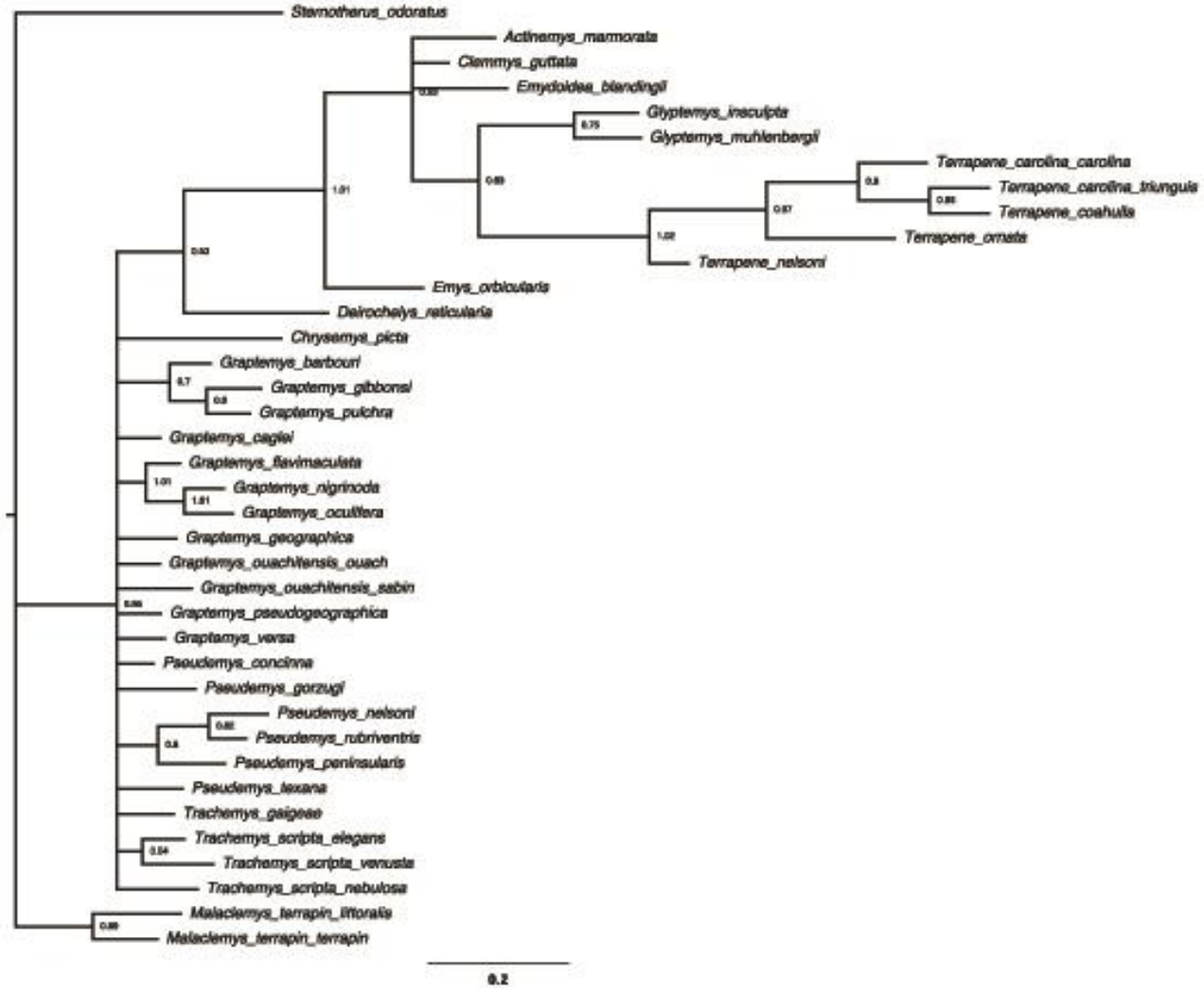
Bayesian analysis with anatomical partitions, branch lengths unlinked, and no additional outgroups. Branch lengths derived from head characters.



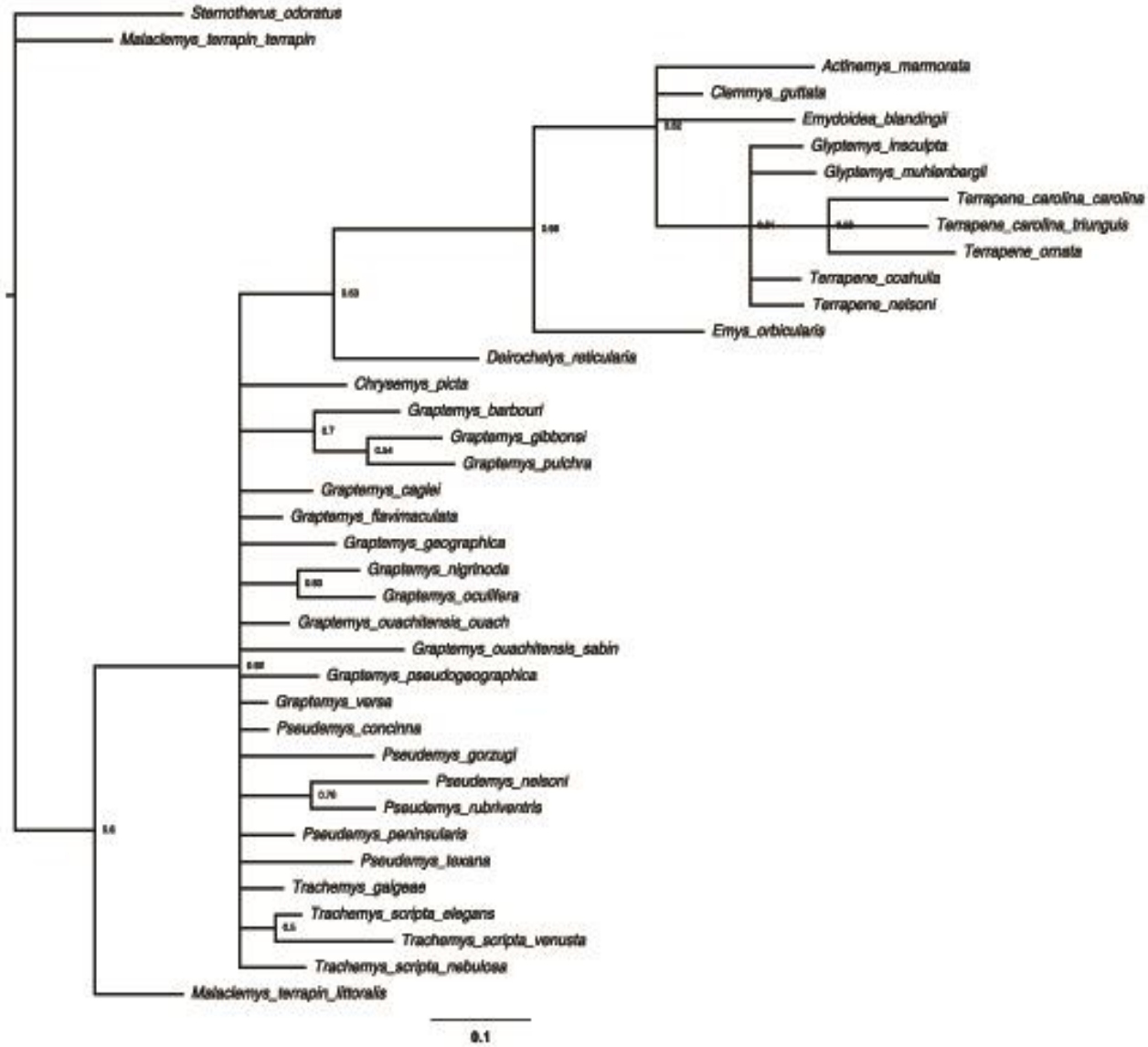
Bayesian analysis with partitions, branch lengths unlinked, and branch lengths derived from shell characters. No additional outgroups.



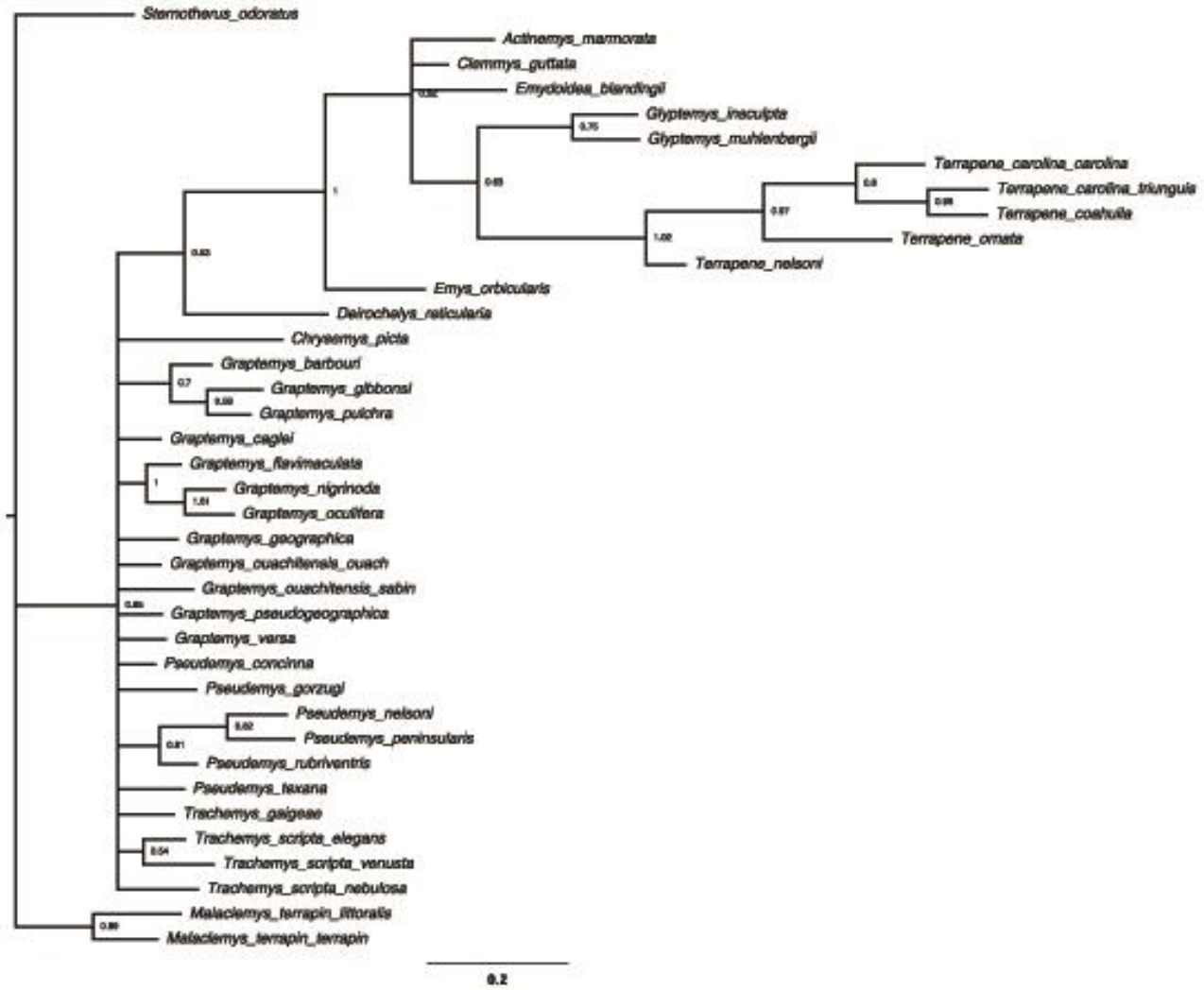
Bayesian analysis with partitions, topology unlinked, and topology derived from head characters. No additional outgroups.



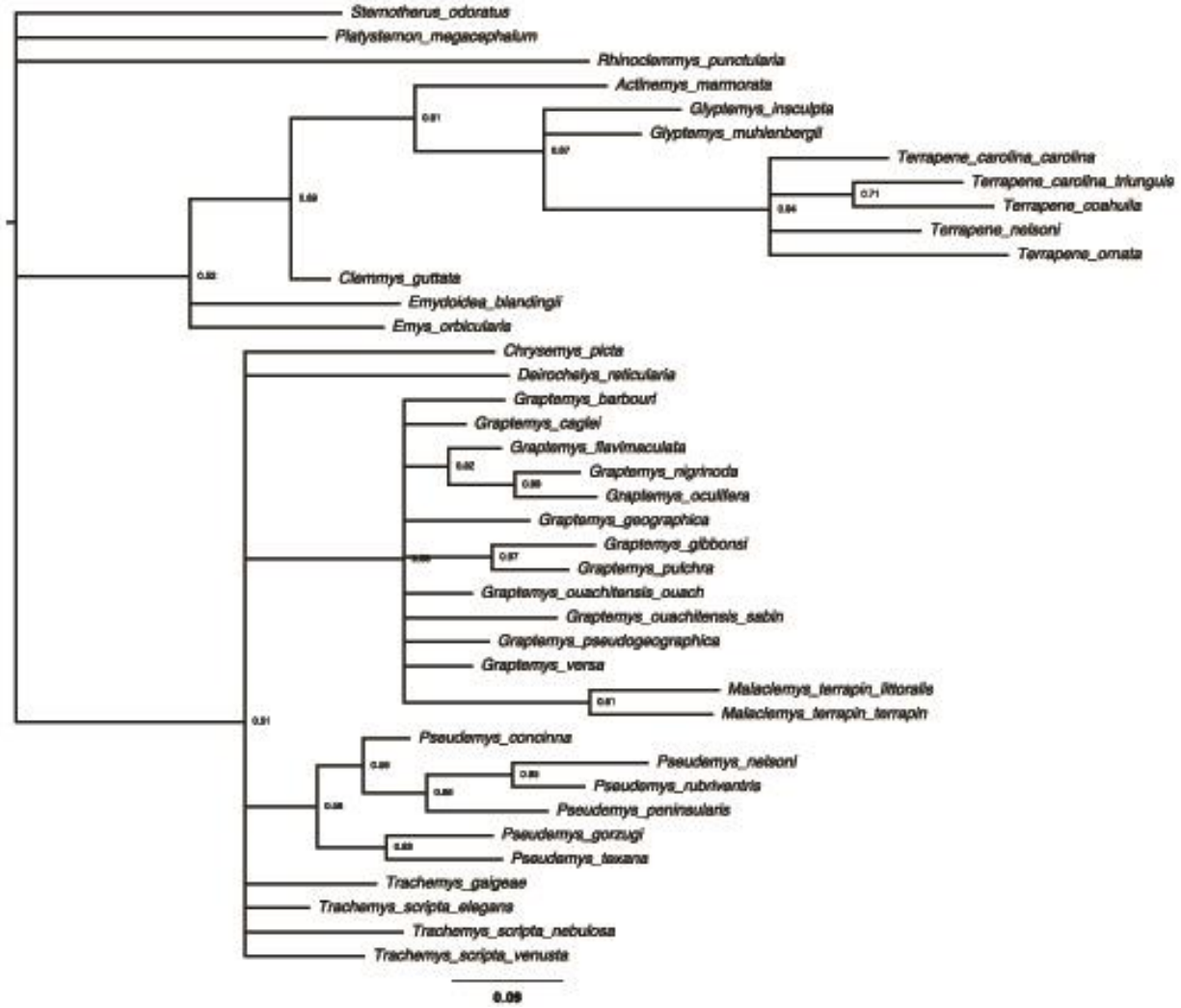
Bayesian analysis, partitioned, with topology unlinked and topology derived from shell characters. No additional outgroups.



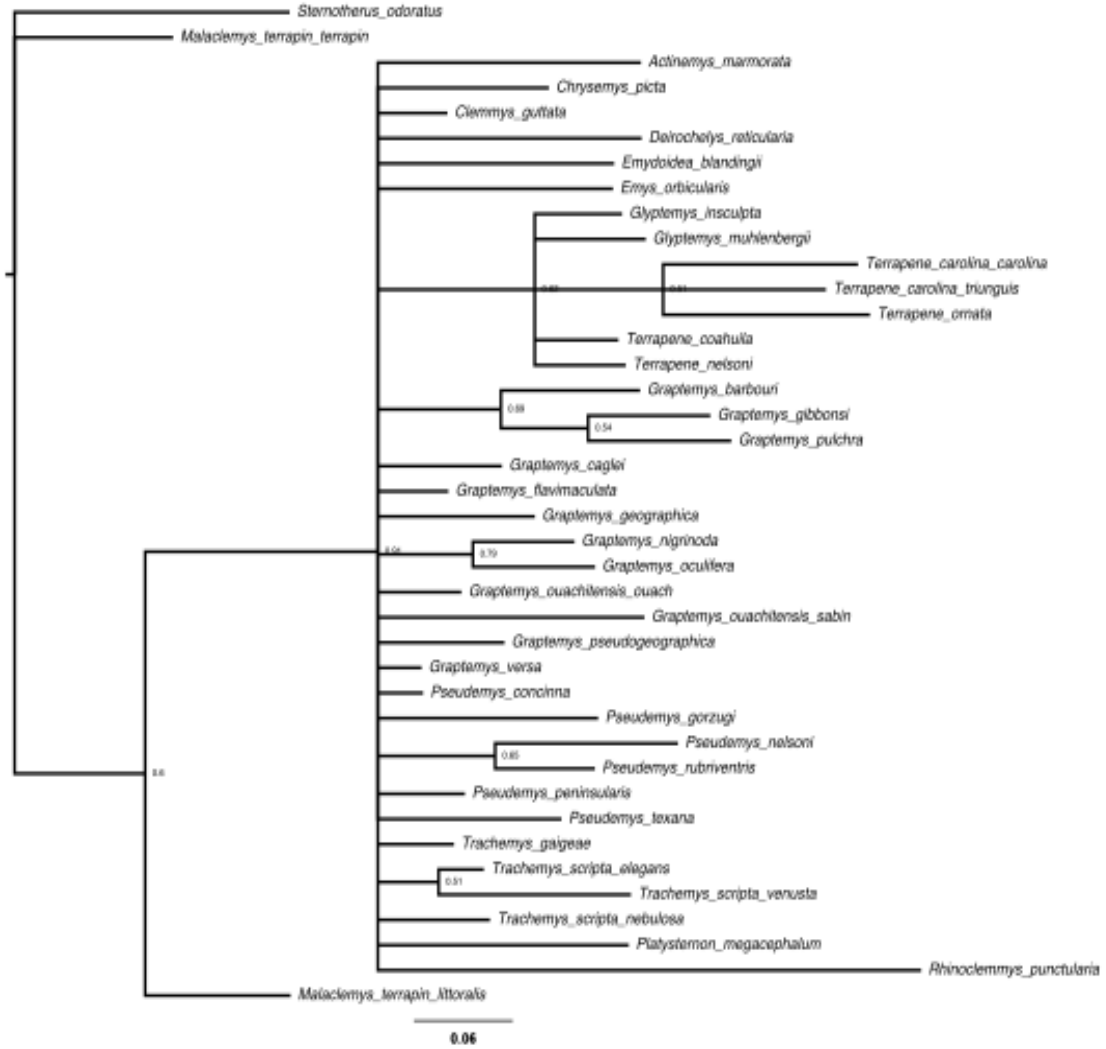
Bayesian partition analysis with branch lengths and topology unlinked, with branch lengths and topology derived from head characters. No additional outgroups.



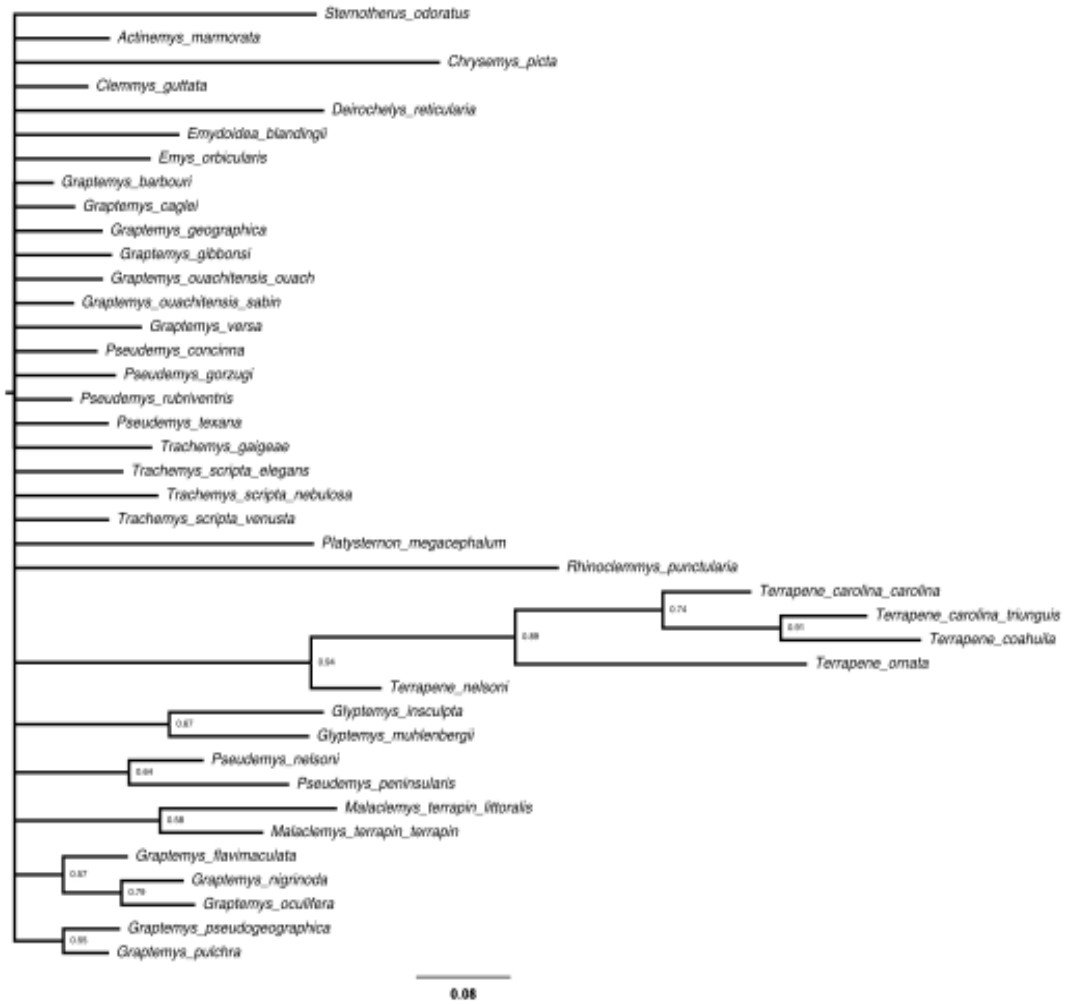
Bayesian partition analysis with branch lengths and topology unlinked, with branch lengths and topology derived from shell characters. No additional outgroups.



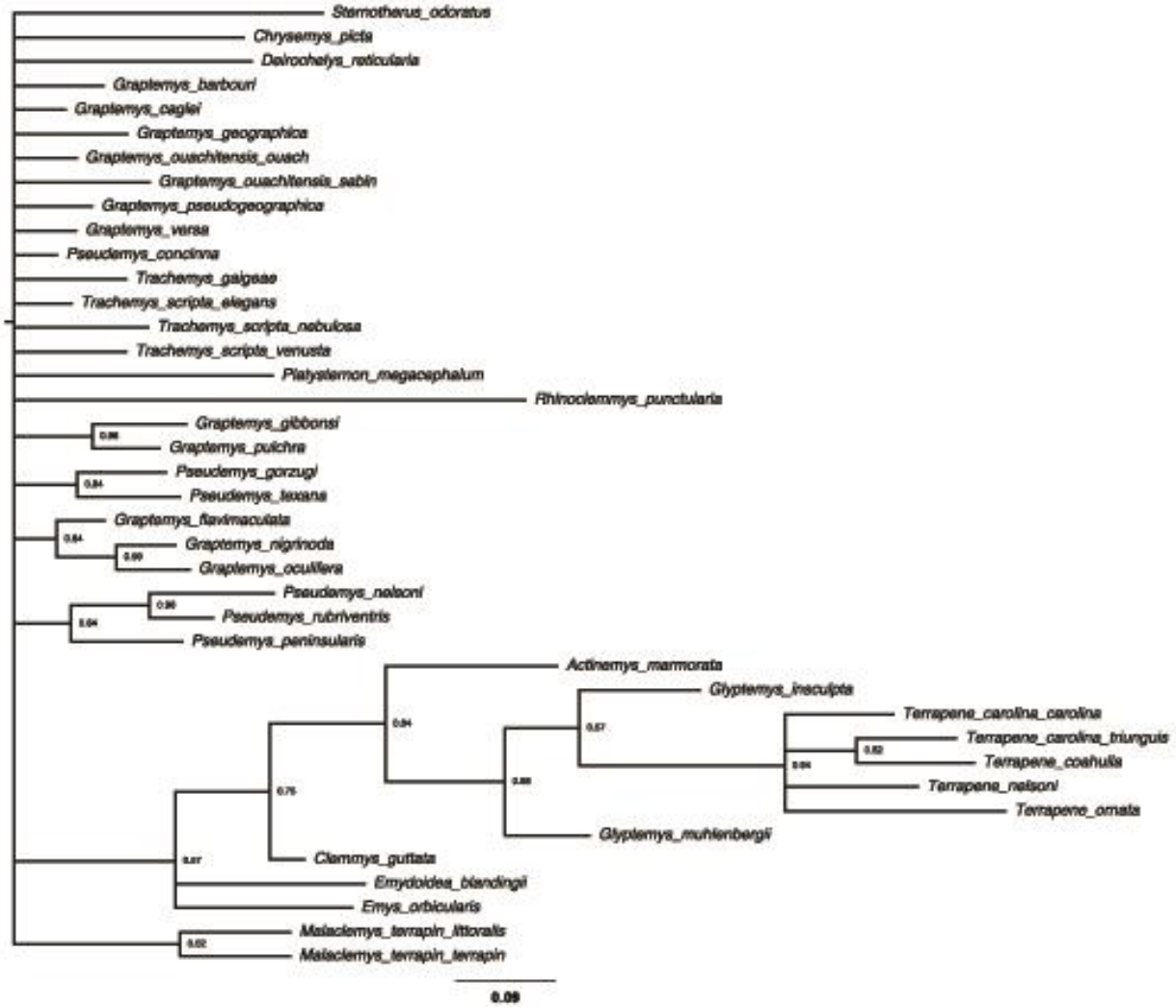
Bayesian analysis, no partitions, with additional outgroups. .



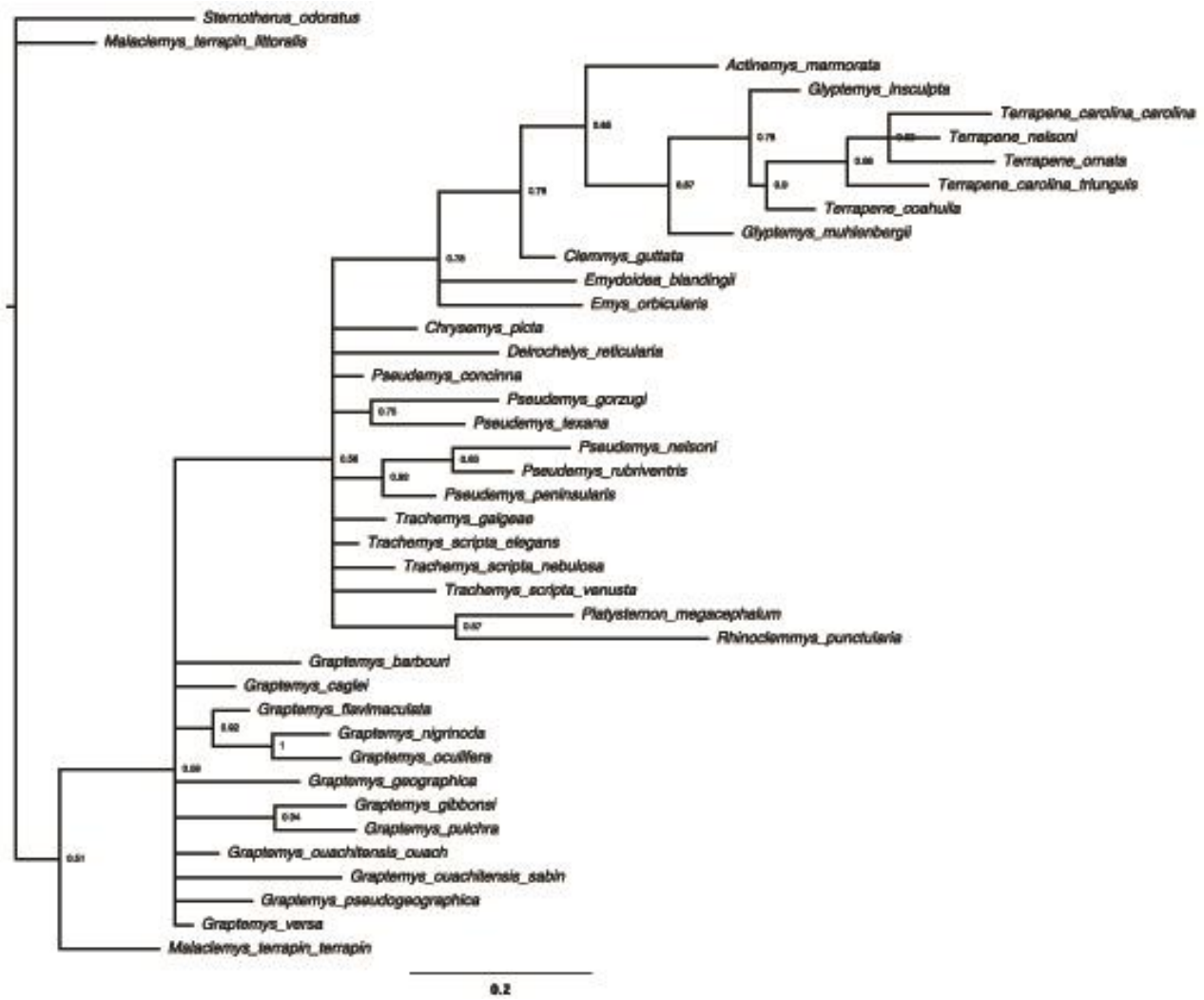
Bayesian analysis using only head characters, with additional outgroups.



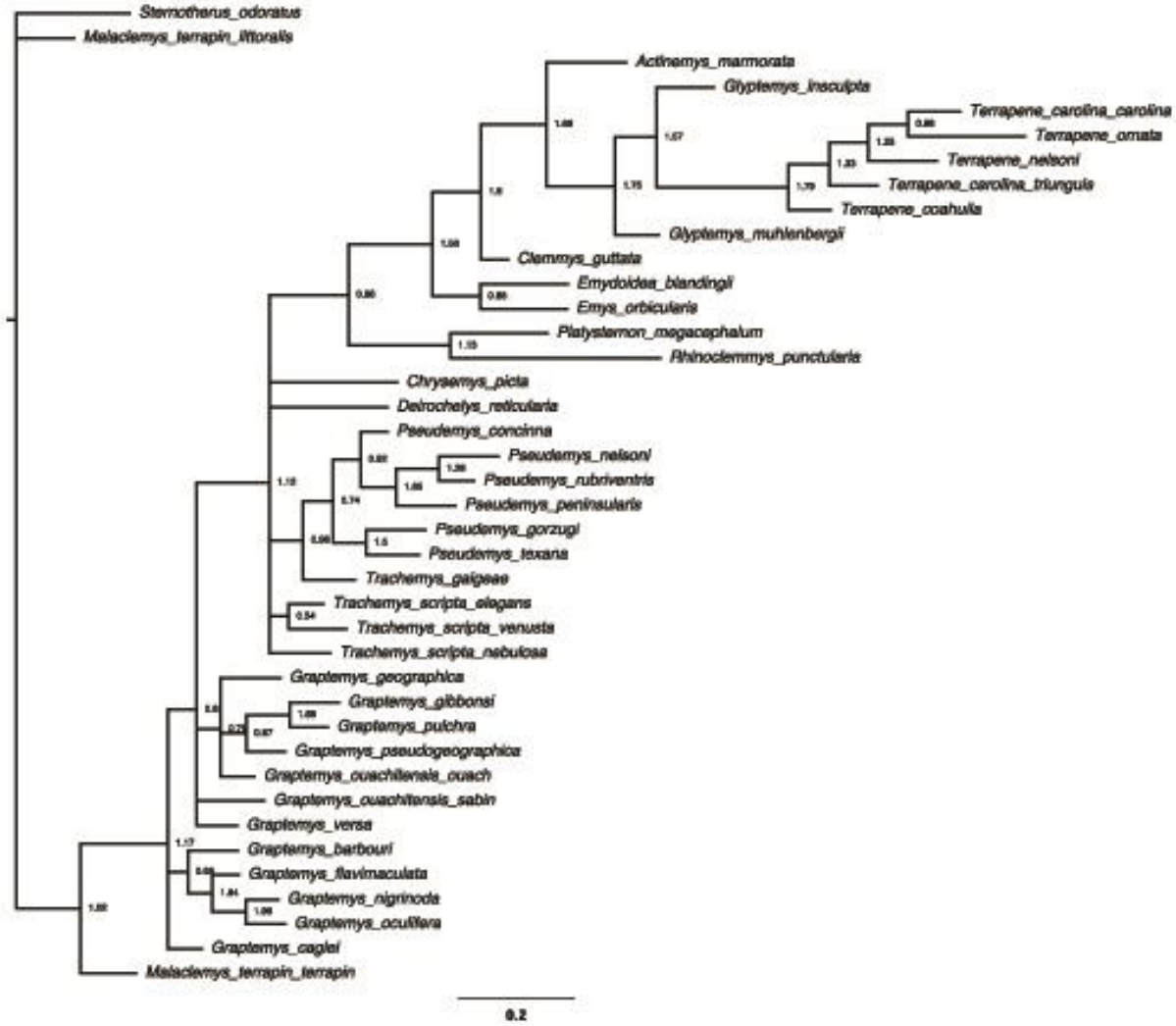
Bayesian analysis of shell characters with additional outgroups added.



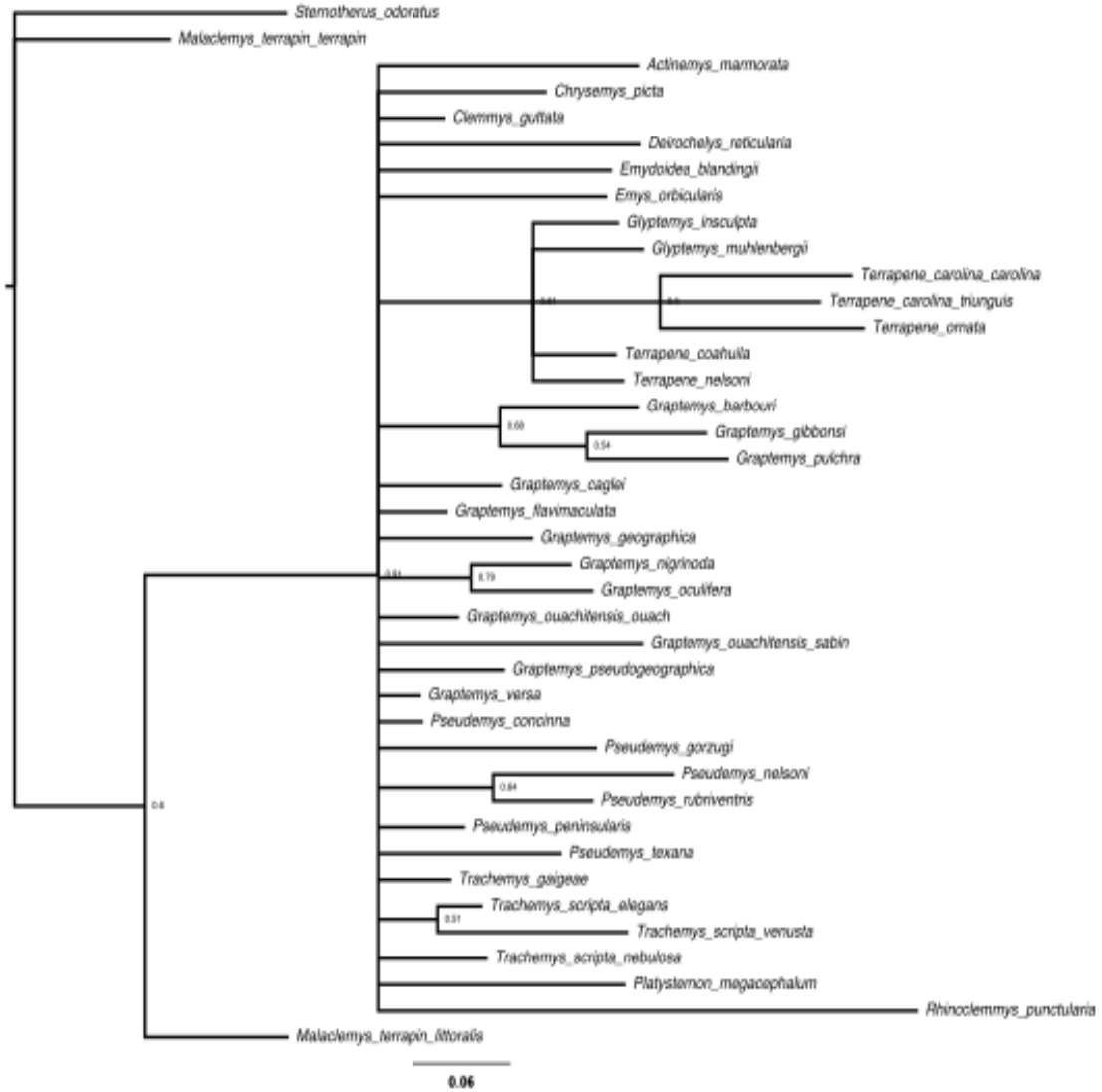
Bayesian analysis, with partitions, all parameters linked, with additional outgroups.



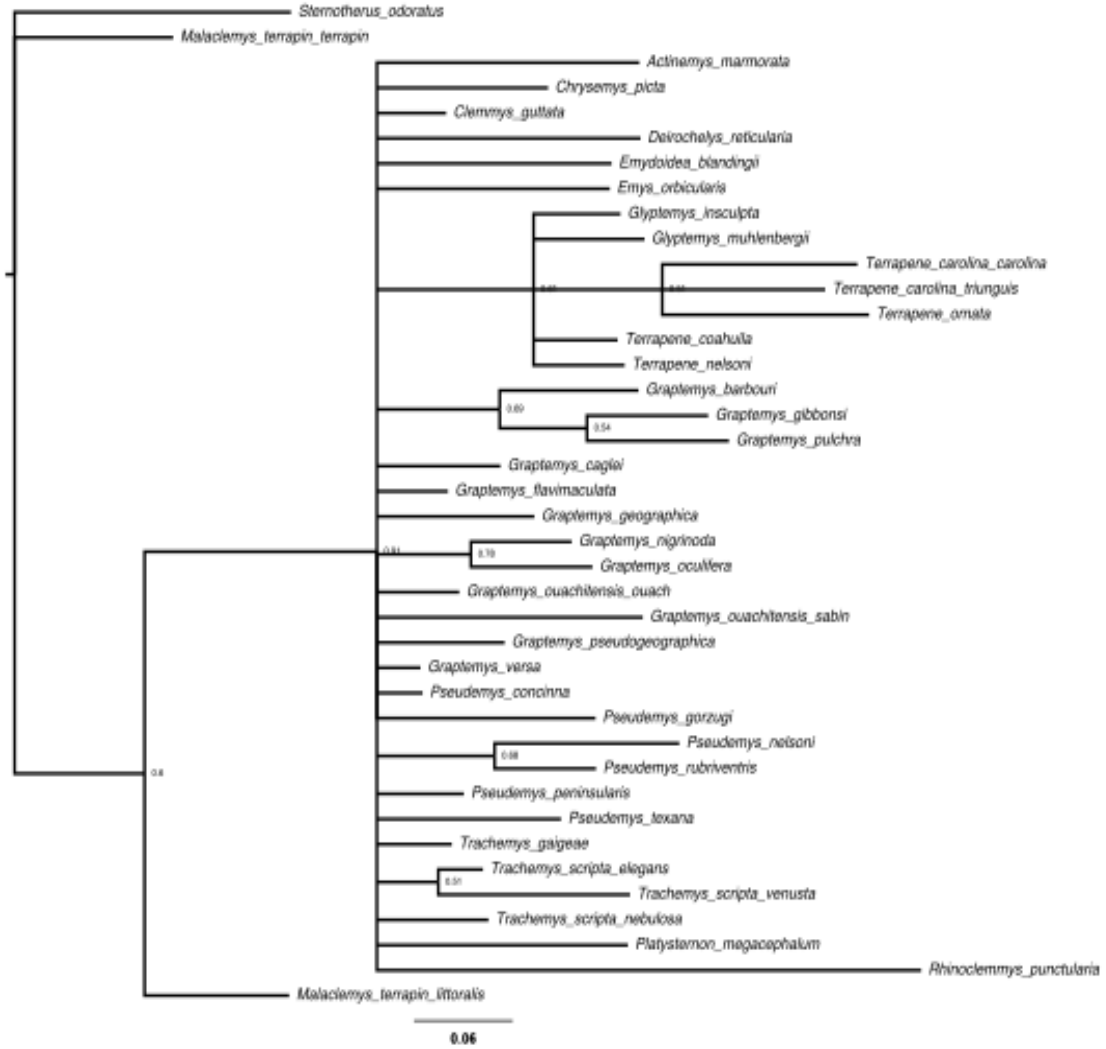
Bayesian partition analysis, with branch lengths unlinked, with additional outgroups, branch lengths derived from head characters.



Bayesian partition analysis with branch lengths unlinked, with additional outgroups, and branch lengths from shell.



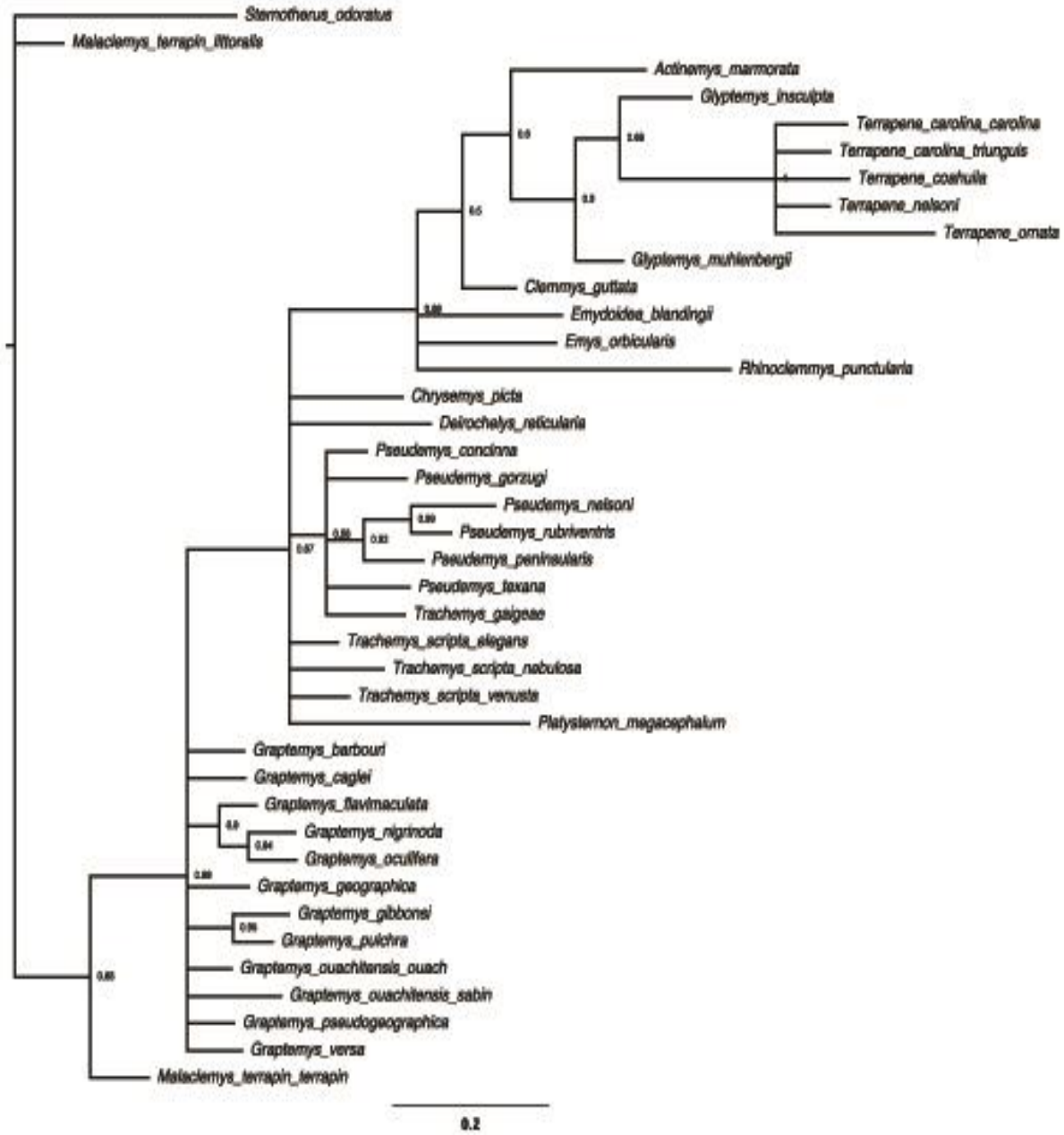
Bayesian partition analysis, with topology unlinked, with additional outgroups, and topology derived from head characters.



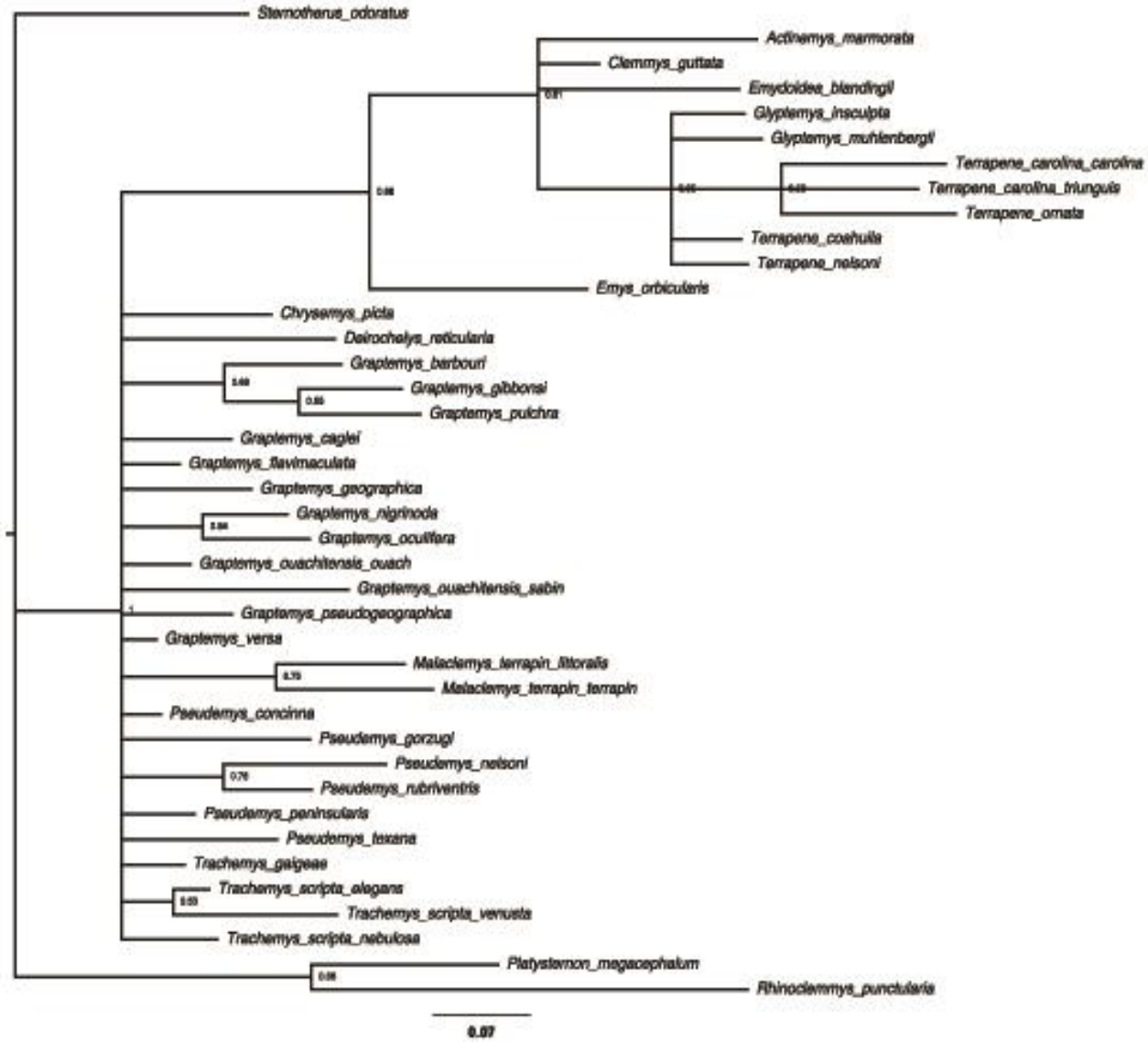
Bayesian partition analysis with branch lengths and topology unlinked, with additional outgroups, and branch lengths and topology derived from head characters.

Bayesian partition analysis with topology unlinked, with additional outgroups, with topology derived from shell characters.

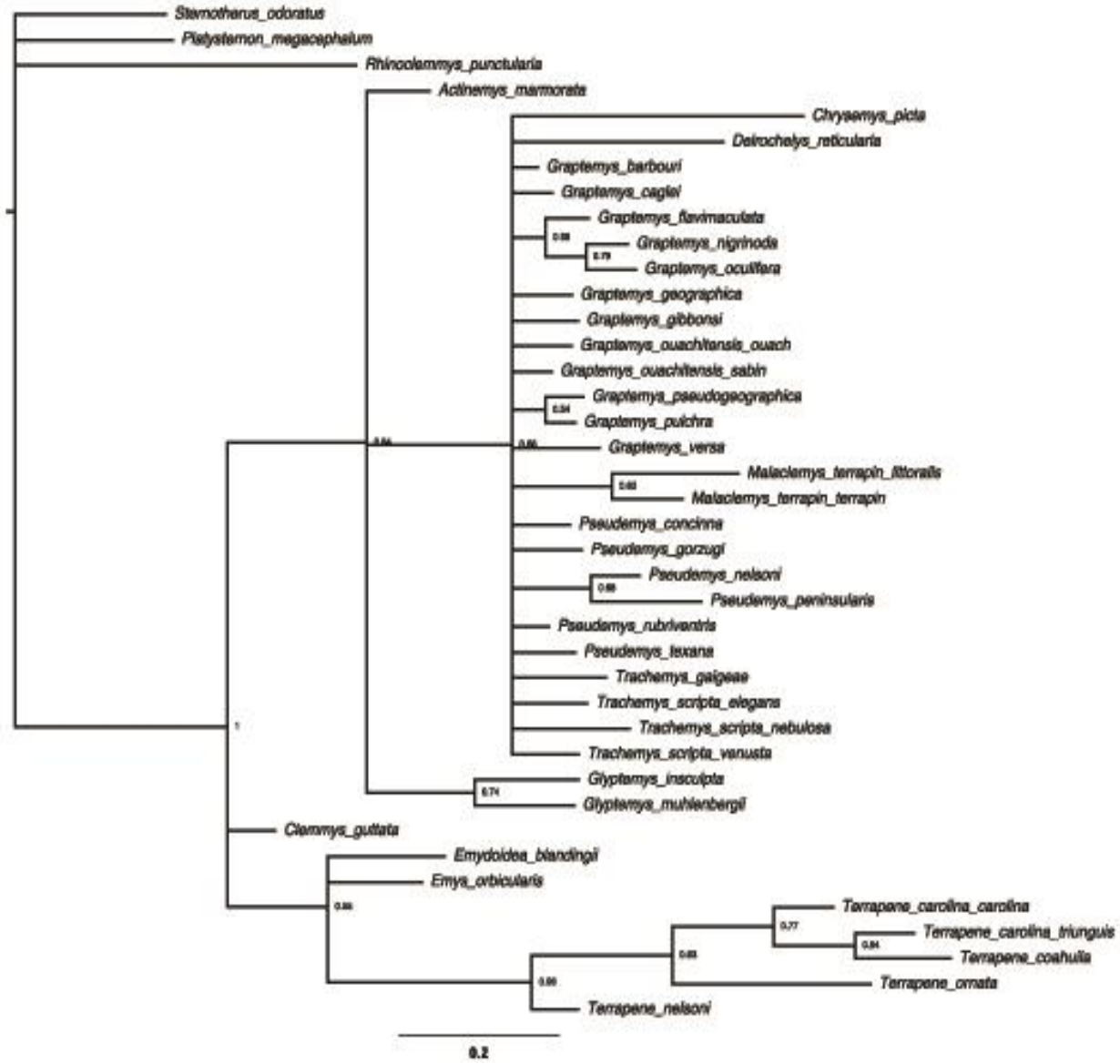
Bayesian partition analysis with branch lengths and topology unlinked, with additional outgroups, and branch lengths and topology derived from shell characters.



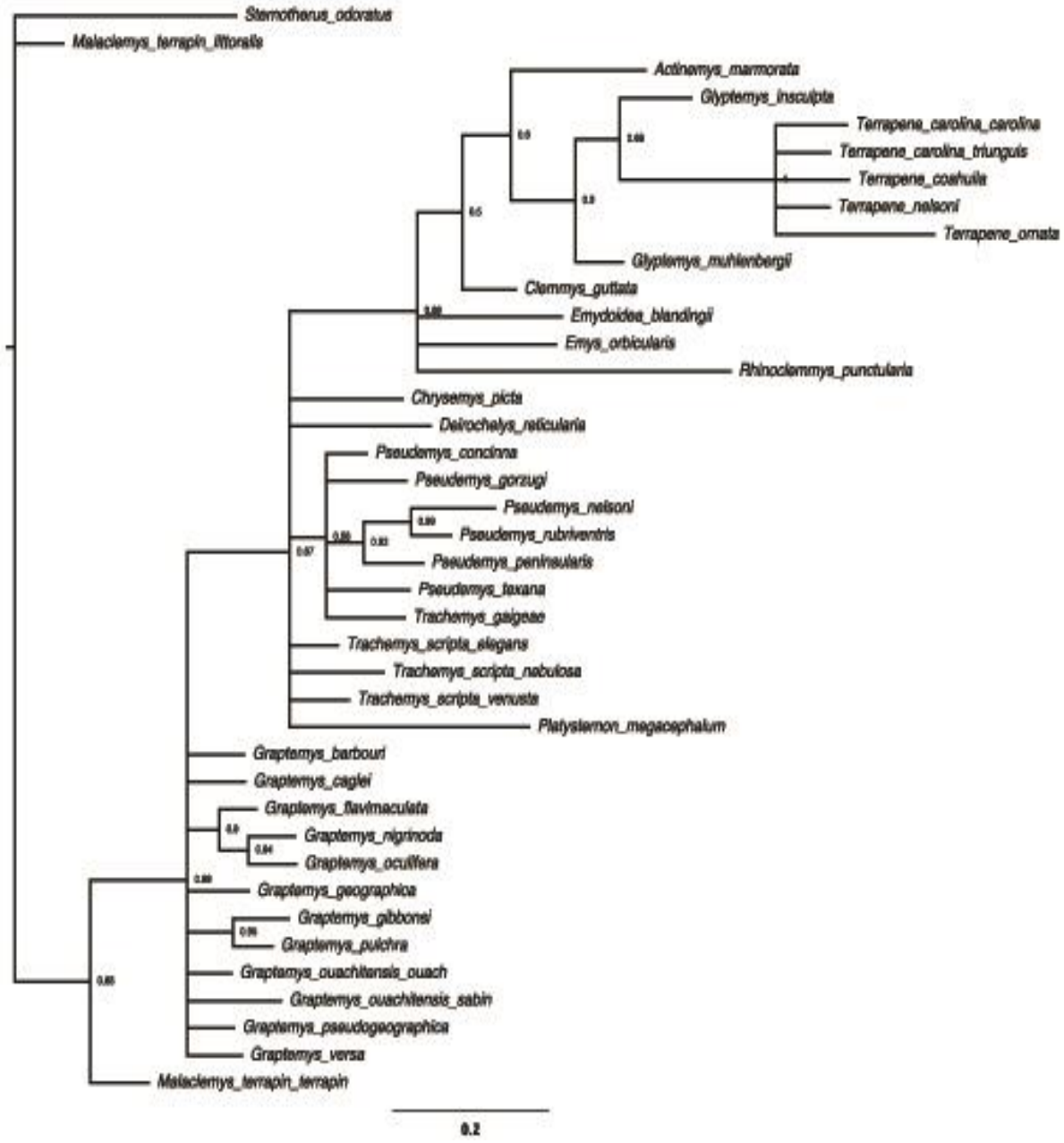
Bayesian analysis with no partitions, with additional outgroups and outgroup constraint.



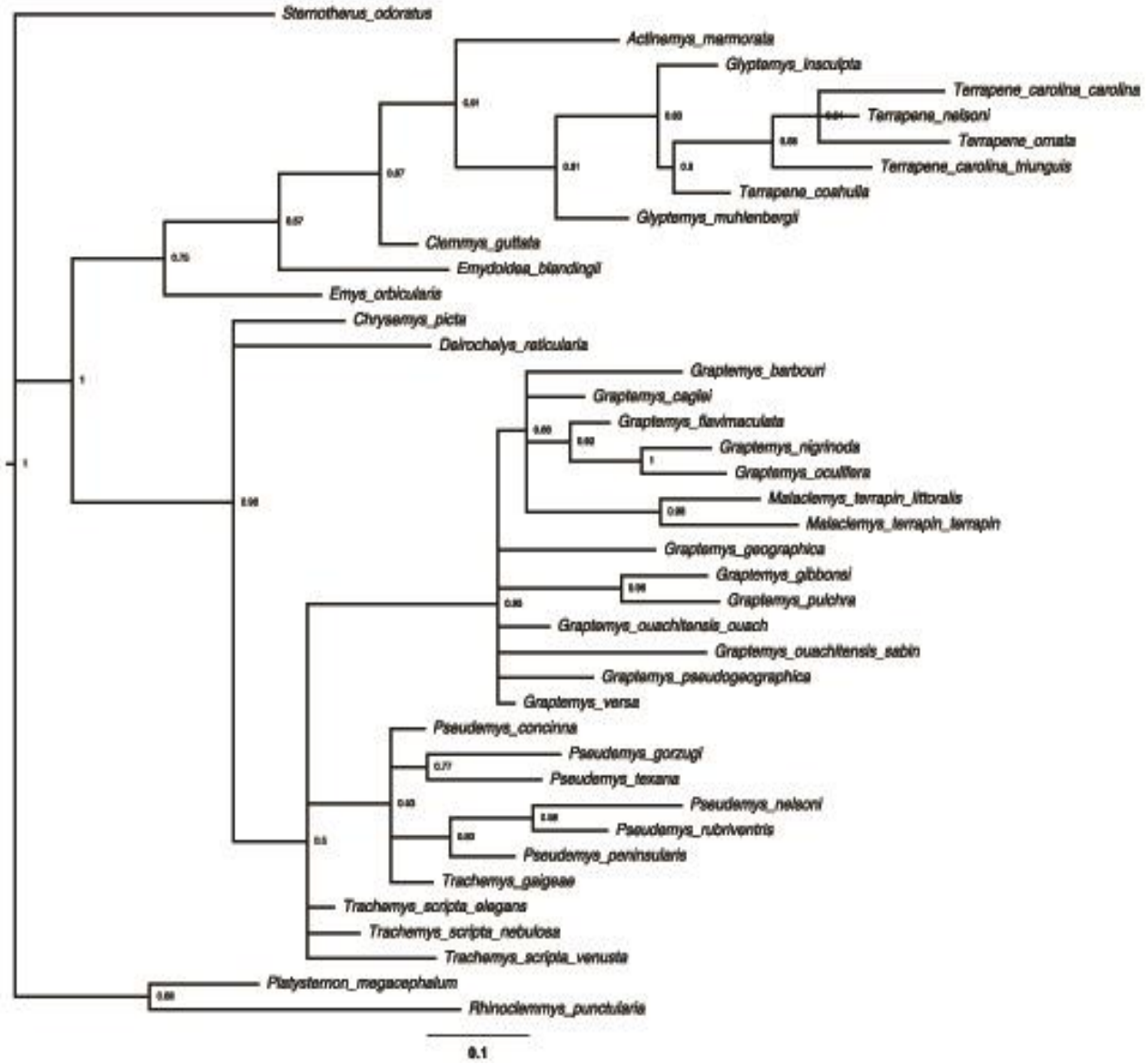
Bayesian analysis of only head characters, with additional outgroups and outgroup constraint.



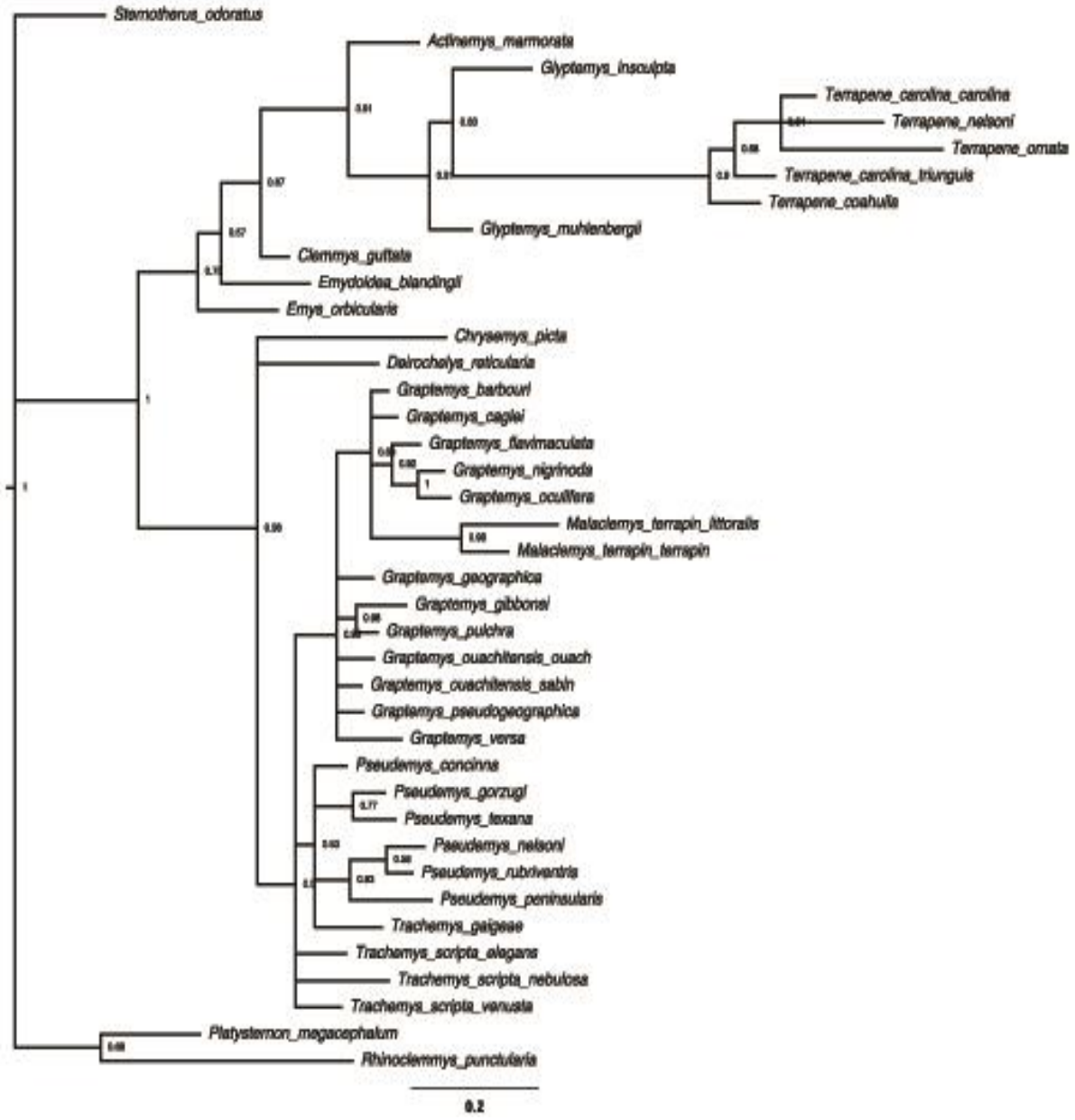
Bayesian analysis of only head characters, with additional outgroups, and outgroup constraint. .



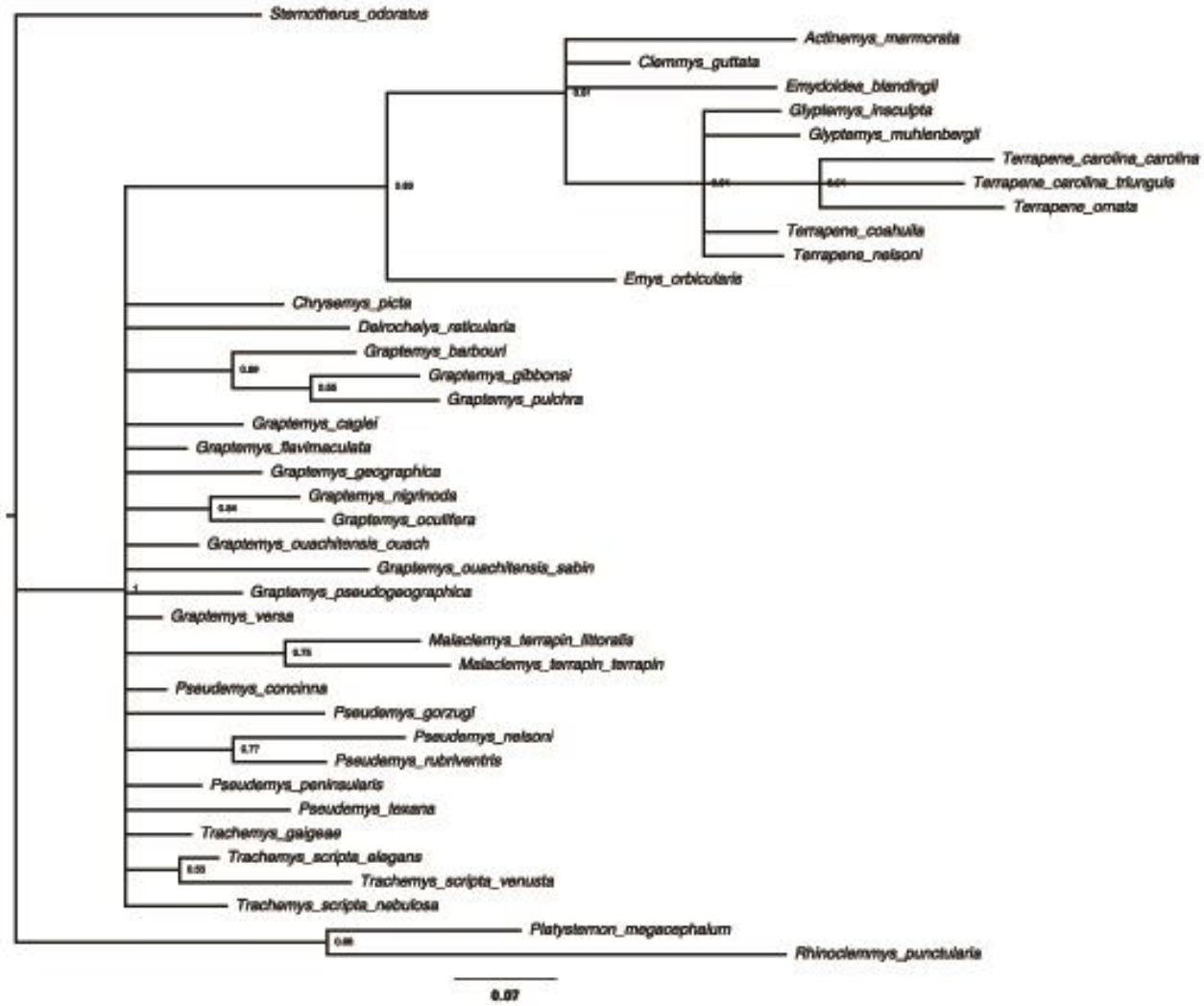
Bayesian partition analysis, all parameters linked, with additional outgroups, and outgroup constraint.



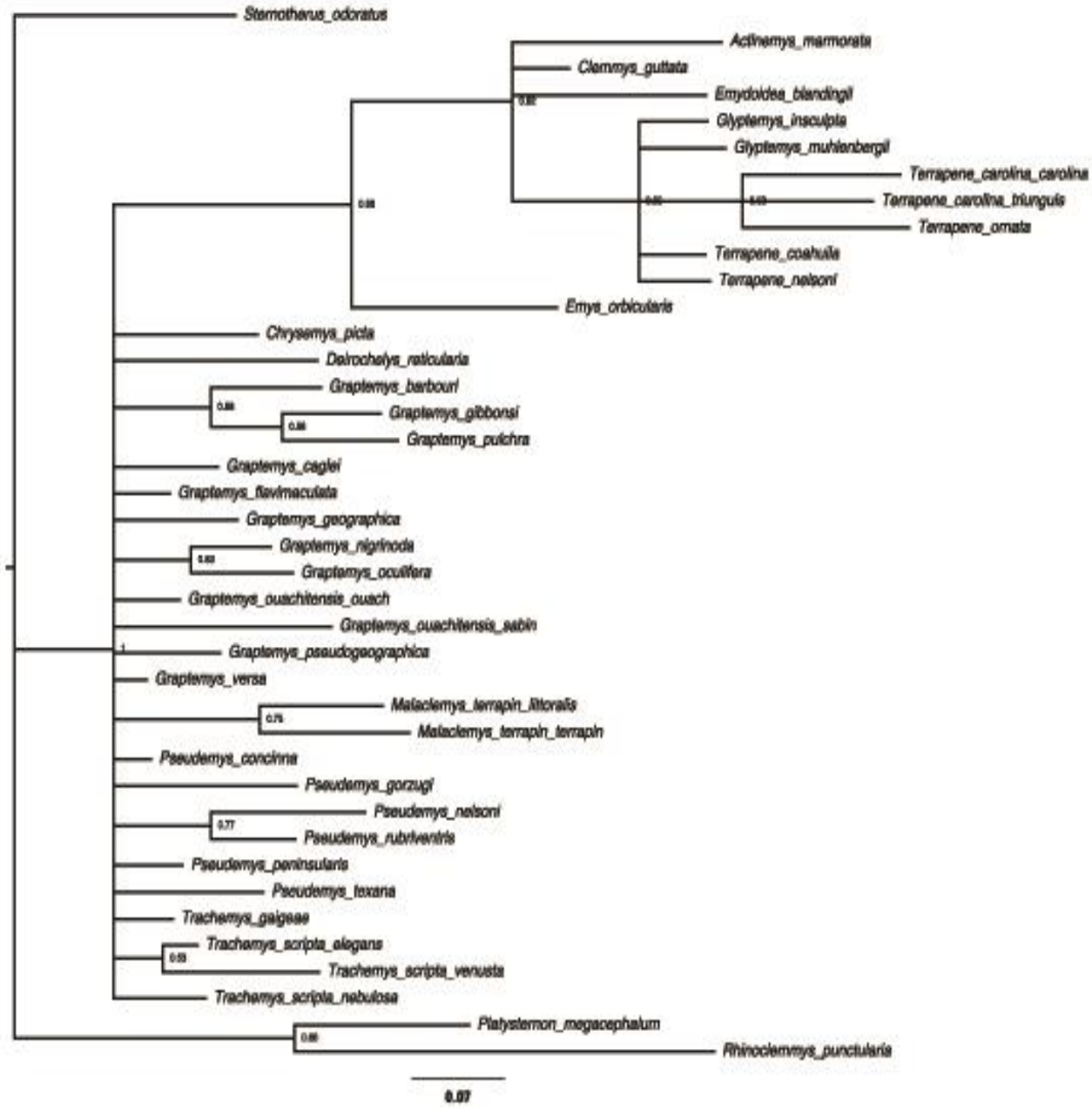
Bayesian partition analysis with branch lengths unlinked, with additional outgroups and outgroup constraint, branch lengths derived from head characters. .



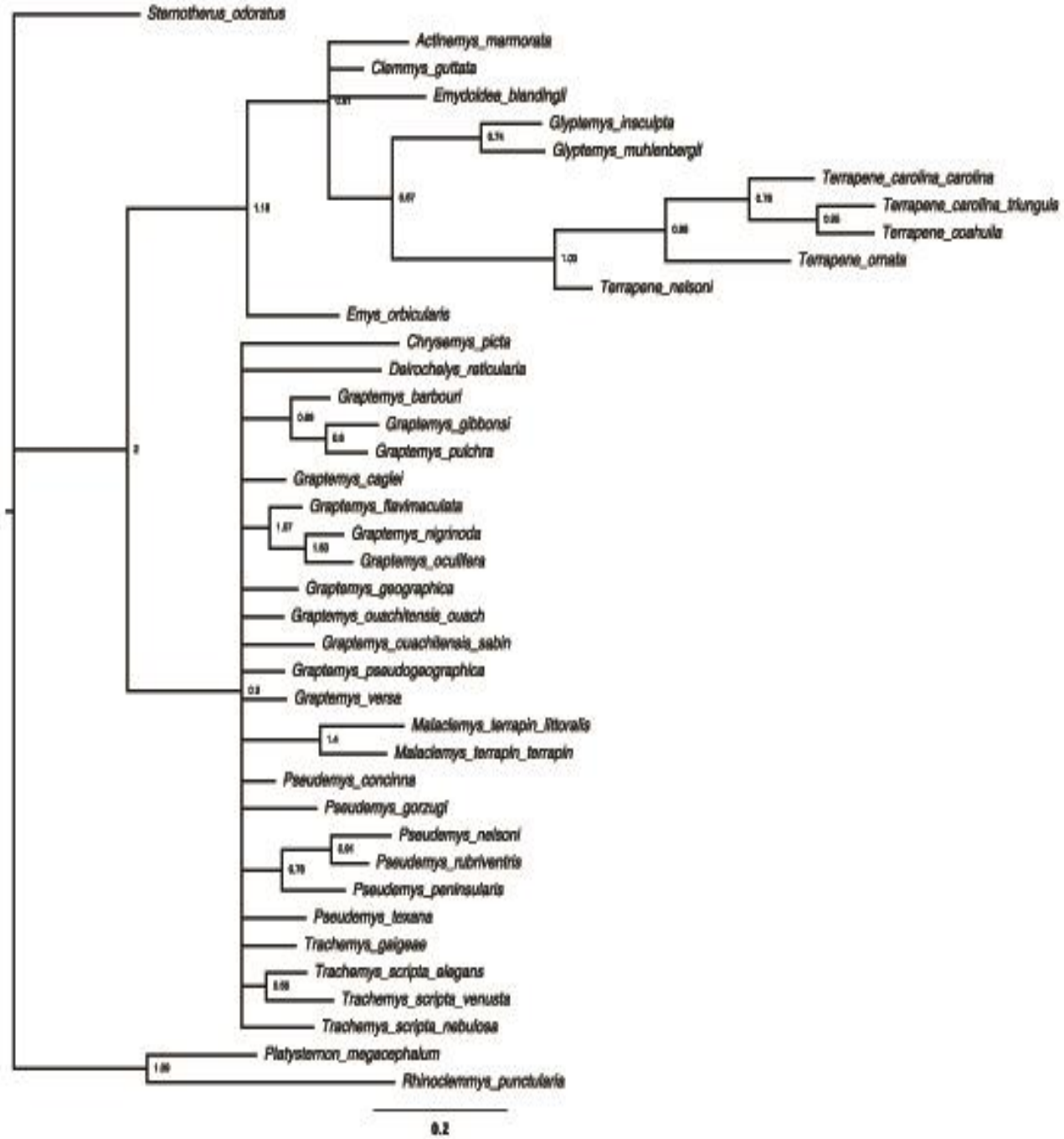
Bayesian partition analysis with branch lengths unlinked, additional outgroups, and outgroup constraint. Branch lengths derived from shell characters. .



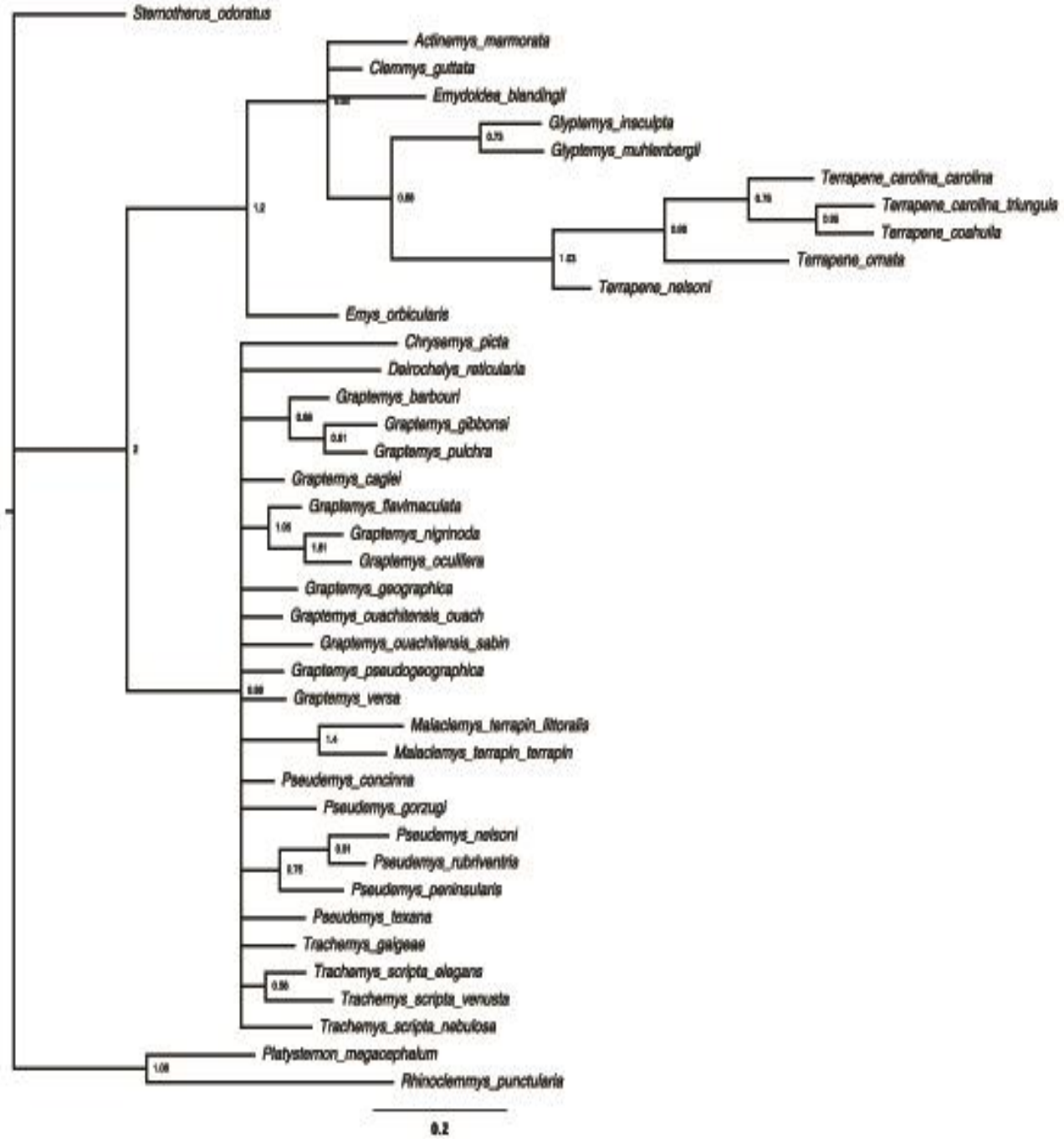
Bayesian partition analysis with topology unlinked, additional outgroups, and outgroup constraint. Topology derived from head characters.



Bayesian partition analysis with topology and branch lengths unlinked, additional outgroups, and outgroup constraint. Branch lengths and topology derived from head characters.



Bayesian partition analysis with topology unlinked, additional outgroups, and outgroup constraint. Topology derived from shell characters. .



Bayesian partition analysis with branch lengths and topology unlinked, with additional outgroups and outgroup constraint. Branch lengths and topology derived from shell characters. .

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